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THE UNIVERSITY OF ALBERTA

AN INVESTIGATION OF THE FOSSIL FLORAS OF THE SMOKY TOWER LOCALITY, ALBERTA.

by

DAVID CHARLES CHRISTOPHEL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL, 1973

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "An Investigation of the Fossil Floras of the Smoky Tower Locality, Alberta", submitted by David Charles Christophel in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Wilson N. Stewart
Supervisor

External Examiner

Date July 24, 1973

ABSTRACT

The strata of the Smoky Tower locality, Alberta, contain two distinct megafloras, a molluscan fauna and at least one microflora. The locality was studied from several approaches based on this diversity.

Over 900 specimens collected from a volcanic tuff horizon at the locality resulted in the identification of nine species, figured in the text, the majority of which are conifers. A revision of fossil *Thujopposites*, *Glyptostrobus* and *Metasequoia* is made based on these specimens and ones from other localities. *Sciadopitophyllum canadense* is reported as the first North American record of attached needles of a *Sciadopitys*-like conifer.

A review of the distinguishing characteristics of fossil *Taxodium*, *Sequoia*, *Metasequoia* and *Glyptostrobus* shows more difficulty is encountered in the separation of the genera than previously thought (Chaney, 1951). In addition to the revision of the descriptions of these genera, the form genus *Taxodiophyllum* is proposed for taxodiaceous remains not assignable to a specific genus.

Over 300 specimens from the siltstone megaflora, located above the tuff horizon, show that this horizon is almost devoid of conifers and dominated by angiosperm leaf remains and remains of aquatic plants. The genera *Cercidiphyllum*, *Zelkova* (or *Ulmus*), *Viburnum* and *Equisetum*

from this horizon are illustrated and discussed. The molluscan fauna and the microflora are shown to yield elements comparable with those from other Paleocene localities.

Collections from the volcanic tuff horizon illustrate a lateral distribution of remains of various genera which is unique to Tertiary localities heretofore described. This distribution is illustrated and various causes are discussed. A possible environmental model is presented and discussed.

Potassium-Argon analysis run on two samples of sanidine and one sample of biotite from the tuff horizon yielded radiometric dates of 62.5, 61.8 and 61.5 million years respectively. Based on these dates and on the identities of the fossils from the various horizons it is concluded that the fossil bearing beds of the Smoky Tower locality are Paleocene in age.

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I wish to express my sincerest gratitude to my supervisor, Professor Wilson N. Stewart, whose supreme ability and enthusiasm as a lecturer first turned my interest to paleobotany, and whose continued encouragement and support have made this thesis possible. I wish to also express my gratitude for his generous allocation of National Research Council funds (#A-4259) to support my research and collecting trips, and to make possible my visit to the University of California, Berkeley, and the University of Oregon, Eugene, for the purpose of studying their collections to aid my research. I would also like to thank the following individuals for the assistance rendered in the preparation of this thesis: Mr. Don Taylor, Curator of Geology, Alberta Provincial Museum and Archives, for his field assistance and for making available the Museum's collections for my study; Dr. C. R. Stelck, Department of Geology, University of Alberta, for assistance in identification of molluscan specimens and stratigraphic interpretations; Dr. H. Baadsgaard and Mr. G. Bonet, Department of Geology, University of Alberta, for radiometric dating of bentonite samples; Dr. S. K. Srivastava, Chevron Oil Research Station, La Habra, California, for assistance in identification of fossil pollen and spores; Dr. J. Wolfe, United States Geological Survey, Menlo Park, California, for assistance in identification of angiosperm remains; Dr. W. L. Fry and

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Finally, I wish to express my deep appreciation to my wife, Annabel, whose quiet encouragement has been a constant source of strength, and whose meticulous editing of the various drafts of this thesis have made possible this final document.

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PREFACE

Where now stand spruce and aspen
Amid fields of waving grain,
Once rose a mighty forest,
Near an infant mountain range
Whose smoking towers belched forth ash
Which fell as snow-white rain,
To blanket all the forest floor
Where leaves and twigs had lain.

And as Time traveled onward,
The mighty forest was no more;
Yet it left behind a memory
Locked within that forest floor.
The snow-white ash had turned to stone,
And the leaves which it contained
Became black carbon silhouettes,
Forever to remain.

The giant trees with spreading boughs
Enjoy the North no more.
The Redwoods and the Ginkgos
Now adorn a distant shore.
Yet their memory lingers onward
As a poem with ageless rhyme -
Black writings on a snow-white page
In the endless book of Time.

The Smoky Tower fossils
Will everafter last;
60 million year reminders
Of Alberta's ancient Past.

CHAPTER 1

INTRODUCTION

The Smoky Tower locality has been known since the early 1960's when the Atlantic Richfield Oil Company began excavation in the vicinity in association with installation of several oil wells. The fossiliferous beds were exposed during this excavation and the associated access road construction. Because of the availability of the aesthetically attractive fossil plants, they were soon collected in quantity by the inhabitants of the area.

During the summers of 1965 and 1966 collections were made by the Alberta Provincial Museum and Archives staff, Edmonton, and a collection of approximately 350 specimens is now housed there. In the spring of 1970 the museum made available this collection to the University for study, and it was at this time that the author began his studies of the material. During the summers of 1970, 1971, and 1972 a collection of approximately 1300 specimens from the Smoky Tower locality was made. This collection, the museum's, and about 50 specimens loaned by various private individuals in Grande Prairie, Alberta, formed the nucleus for the research project.

The primary emphasis of the study is a systematic analysis of the two megafloras that occur at the outcrop, with particular attention given to the lower flora, and

specifically to the family Taxodiaceae, which is well represented in the latter. The stratigraphy, selective deposition, radio-chronology, and paleoecology of the locality are treated as accessory topics.

All botanical terms, when not specifically defined within the thesis text, are used as defined in Swartz (1971). All specimens figured in the text are deposited, unless stated to the contrary in the figure descriptions on the pages facing the figures, in the paleobotanical collection, Department of Botany, University of Alberta, Edmonton.

CHAPTER 2

GEOGRAPHY AND STRATIGRAPHY

The Smoky Tower locality is approximately 80 miles south and east of Grande Prairie, Alberta. More specifically, it is located between mile 66 and mile 67 of the Goodwin-Hinton Forestry Trunk Road south of Goodwin (Text-Fig. 1). The precise legal description of the locality (as may be seen on the sign in Figure 1) is LSD 10- 6 - 63 - 2 - W6.

Figure 1 also shows a general view of the locality, with the photograph taken looking east. The tuff bed containing the major coniferous flora is indicated by the letter T, while the plant fossil bearing siltstone horizon is indicated by S in the same figure. The hill in Figure 1 is flanked on either side by hills of a similar size, both containing the fossil bearing strata. However, the tuff horizon in the adjacent hills has proven to be almost totally barren of fossil remains.

Text-Figure 2 shows a partial section of the exposure with the position of the various fossil bearing strata indicated in the appropriate places. The detail of the section was taken from the area marked SS in Figure 1. The exposed strata are not sufficiently extensive to enable stratigraphic correlations to be made. Therefore, only a limited section sufficient to show the relative position of

the plant-bearing beds is given.

Examination of the drilling logs for the oil well shown in the foreground in Figure 1 enabled the fossil bearing strata to be formally located in the stratigraphic column.[1] Examination of the data from these logs shows that the plant fossil bearing tuff bed is 4902 feet above the base of the Wapiti Formation. This is not inconsistent with the lower Paleocene age determined by radiometric means for the bentonite in the tuff horizon. No evidence of the earlier Kneehills Tuff appears in the logs, but as logging was started at a depth of 756 feet, it is possible that the Kneehills Tuff would be found in the unlogged upper portion of the well. It is of course also possible that the Kneehills Tuff bed, which is a significant marker bed in southern and central Alberta (Irish, 1970), does not extend to the area of this locality.

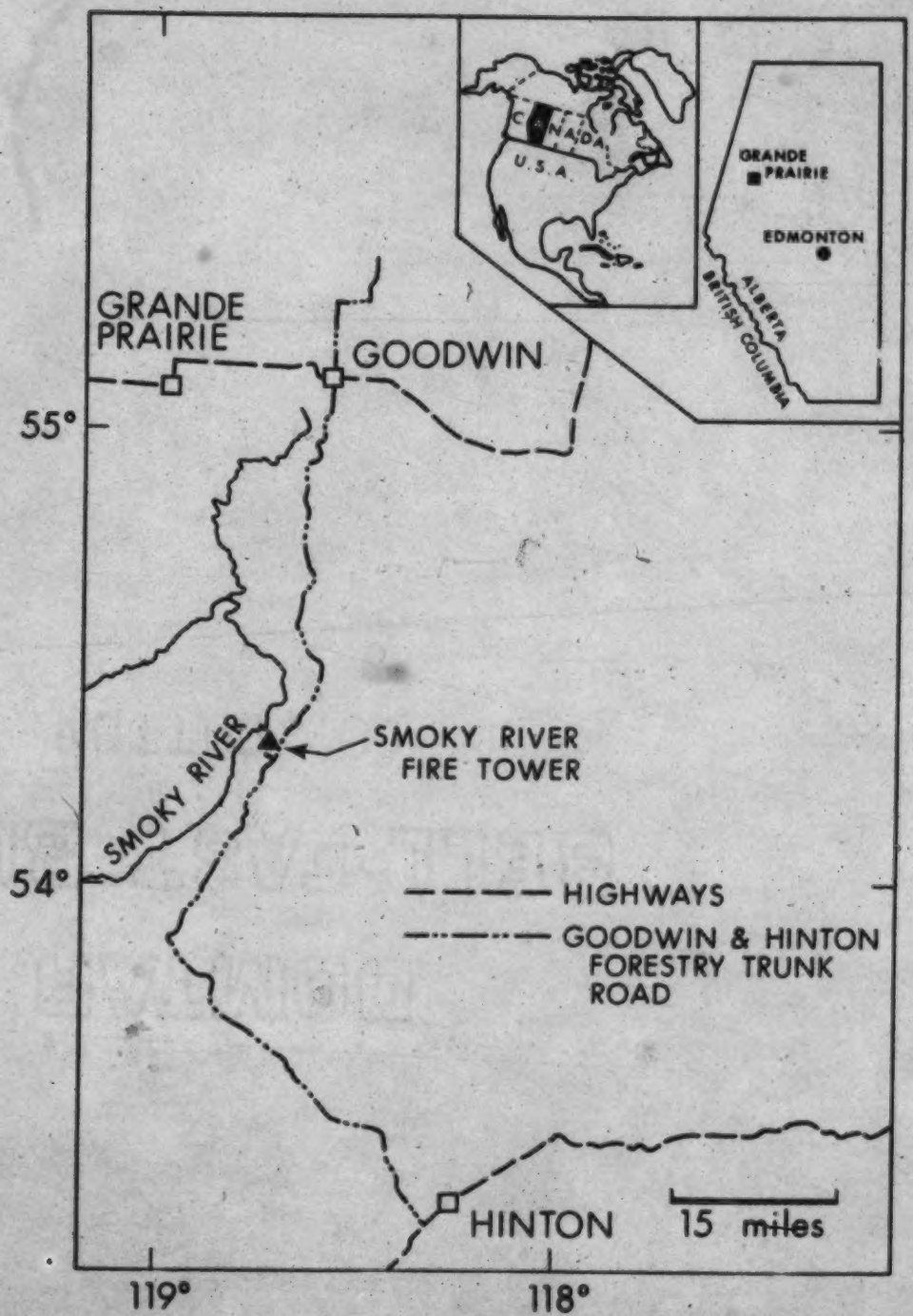
The lateral extent of the fossil bearing beds is unknown at this time. The only other known outcrop of the tuff horizon occurs approximately one-half mile farther south on the forestry trunk road on the east side of the road. A short access road was constructed in this area, exposing a very limited outcrop of the tuff horizon. A small collection was made from this area, but in general the fossils are not well preserved and the matrix is badly

---

[1] The drilling log and its interpretations are officially recorded in the "Schedule of Wells Drilled for Oil and Gas - Province of Alberta," 1963, published by the Oil and Gas Conservation Board, Calgary, Alberta.

weathered. The few specimens from this secondary site which are mentioned or figured in the systematic portion of this thesis will be labeled as coming from "Locality B".

Dr. J. Campbell, Research Council of Alberta, stated (personal communication) that test drillings 3-5 miles east of the locality failed to give any evidence of the tuff layer, and also that outcrops along the Smoky River, west of the locality (Text-Fig. 1) do not show any evidence of the fossil bearing tuff layer. Based on these observations it may be concluded that the tuff bed has a fairly limited lateral extension, due either to depositional or later erosional factors. However, only intensive drilling and surveying of the area will provide precise information on the extent of the horizon.



TEXT-FIGURE 1.

FIGURES 1-3.

Fig. 1. View of the Smoky Tower locality looking east. Large letters A - D indicate lateral positions along the tuff horizon. They correspond to the positions indicated by the same letters in Figs. 126-127, and in Text-Fig. 6; SS represents the area at which the section shown in Text-Fig. 2 was measured; T indicates the fossil bearing tuff horizon; S indicates the fossil bearing siltstone horizon. The sign on the well head reads:

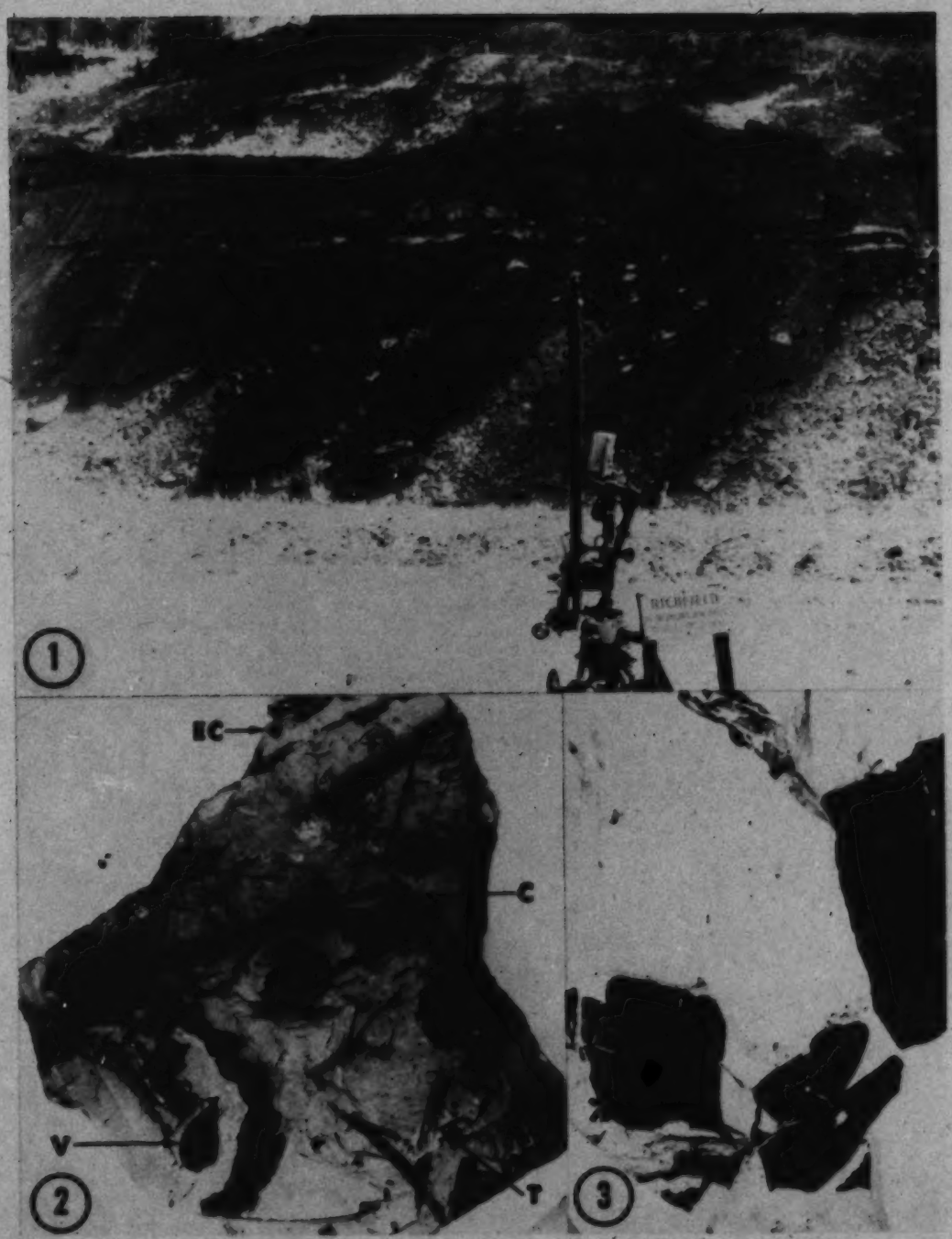
RICHFIELD

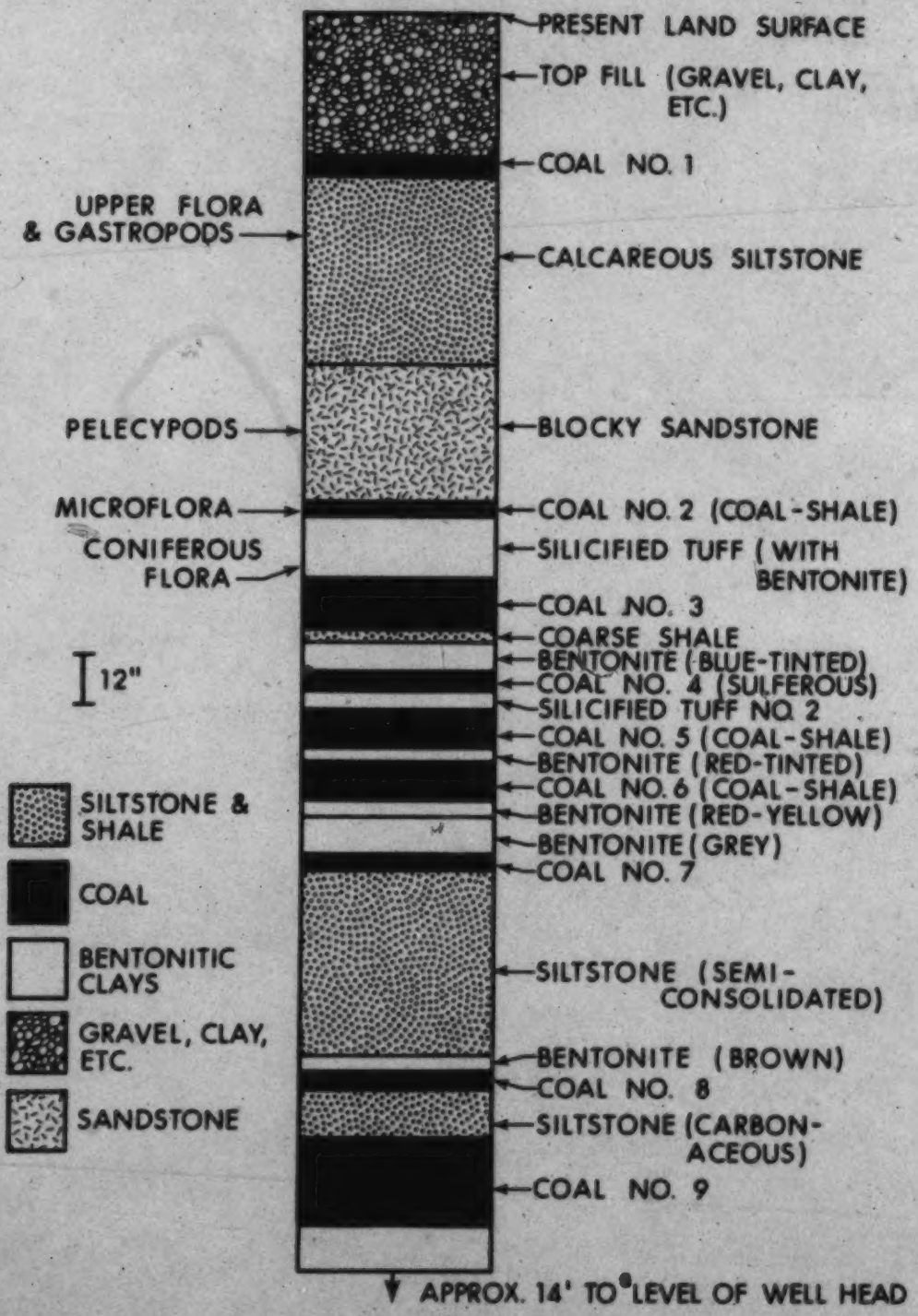
R.O. CORP SINCLAIR A LATOR 10-6-63-2

LSD 10-6-63-2-W6

Fig. 2. Specimen S3806 - material from the siltstone horizon showing various fossil taxa. EC indicates an *Equisetum* cross section; C indicates a *Cercidiphyllum* leaf; T indicates *Typha*-like monocot leaf fragments; V indicates a *Viburnum* leaf. X 0.5

Fig. 3. Specimen S2733A - material from the tuff horizon showing two *Ginkgo* leaves with varying degrees of lobing and a fragment of a *Platanus* leaf. X 0.6


1
EC
C
V
T
2
3



TEXT-FIGURE 2. A partial section of the Smoky Tower locality, Alberta.

CHAPTER 3

MATERIALS AND METHODS

Materials

Fossil Material - The fossil material at the Smoky Tower locality was found in three distinct horizons and will be treated descriptively and procedurally as separate entities. The lowest of the three horizons, known as the tuff layer (Text-Fig. 2), consists of pockets of silicified volcanic ash grading into unconsolidated bentonite. Highly carbonized plant compressions are in evidence throughout the stratum, but it is only possible to work with those in lenses of consolidated, silicified bentonitic tuff. The silicified matrix exhibits a conchoidal fracture, and therefore it is only in rare instances that both an impression and compression of the same fossil are obtained.

Because of the white matrix, the carbonized remains are readily visible (Fig. 3). However, higher magnification shows that the degree of preservation is not as good as the superficial observation would indicate. In the case of angiosperm leaves usually only primary and secondary venation is observable, with only the rare occurrence of smaller veins. Fortunately, the majority of the flora is gymnospermous, and taxonomy here is more dependent upon leaf shape, size, attachment and position; all of which are

readily discernible in the specimens.

As has been the case in many other Tertiary floras, e.g. the Florissant flora (MacGinite, 1953) and the Genesee flora (Chandrasekharam, 1972), where preservation is associated with volcanic ash, there is often an absence of preserved cuticle. Such is the case with the tuff flora at the Smoky Tower locality, and all techniques attempted for the recovery of cuticle were unsuccessful. This phenomenon has often been attributed to the alkaline nature of the rock matrix which causes degradation of cuticle. Chandrasekharam (1972) noted that the cuticle of *Carcidiphyllum* was completely removed in one week by a 2% solution of sodium hydroxide. In terms of solutions in nature however, 2% is still extremely alkaline. Further experiments were therefore carried out using more dilute solutions, and it was found that by using a 0.01% solution of sodium hydroxide the cuticle was completely removed from *Metasequoia* in a period of ten months. A similar experiment with *Sciadopitys* needles showed total removal in just over one year.

To further test the hypothesis that an alkaline matrix might be responsible for the disappearance of cuticles, samples of the bentonite surrounding the fossiliferous tuff were suspended in distilled water having a pH of 7. The pH of the suspension was then checked immediately, and subsequently at weekly intervals for a period of a month. The initial check yielded a pH of just under 7.1 (less alkaline than the 0.01% test solution by a factor greater

than ten thousand), while checks during the progressive time period showed no alteration. This experiment, then, did show the matrix to be slightly alkaline, but it is experimentally impossible to say whether such a low concentration of hydroxide ions would ever cause the degradation of cuticle. It may be concluded from the experiments that if alkalinity is responsible for the lack of cuticle, it was not accomplished in recent years. It is of course possible that the pH was much higher at the time of the ash deposition, and has subsequently been lowered either by leaching or by neutralization by natural acids.

The other megafossil bearing stratum, labeled Calcareous Siltstone in Text-Figure 2, contains a flora high in angiosperm leaf remains and virtually devoid of conifers. The coloration of the matrix here ranges from dark gray to buff, and thus provides less contrast with the fossils than in the white tuff layer (Figs. 2, 3). The matrix displays well-defined, parallel bedding planes, but the degree of consolidation is extremely variable with the result that many specimens are extremely fragile. Preservation is better than in the tuff layer, with many angiosperm leaves showing good tertiary venation (Fig. 115). Although there is no evidence of inclusion of volcanic ash in the matrix, the plant remains, as in the tuff layer, are totally devoid of cuticle.

Between the two plant megafossil beds is a thin layer of coaly shale varying from 1-4 inches in thickness. This

layer contains a rich, though not extremely diverse, microflora which will be discussed in the next chapter. This flora shows little if any correlation with the megafloras above and below it. Using techniques described later both megaflora horizons were examined for microfossils and found almost totally devoid of them.

Living Material - In many instances, accurate identification of fossil materials of this age can only be made by direct comparison with extant material. This is especially true when an attempt is made, as in this thesis, to delineate genera and species almost entirely on vegetative remains. It is fortunate that the greenhouses of the University of Alberta have an excellent collection of young conifers, and thorough use was made of this material. In addition, it was possible to study and sample mature living specimens of *Sequoia*, *Metasequoia*, and *Taxodium* at the University of California, Berkeley, and mature *Cryptomeria* at the Botanic Garden, University of Washington. In addition, herbarium material representing various taxodiaceous genera was received from the Arnold Arboretum, New York Botanic Garden, and the University of California, Berkeley.

Methods

Because of the conchoidal fracture of the volcanic tuff, entire leaf specimens were initially seldom exposed. Thus it became necessary to expose the fossils remaining

embedded in the matrix by mechanical means. The most satisfactory method was found to be a jeweler's Vibrograver, using a standard diamond point for the coarse work and a phonograph needle attachment for the more delicate completion (Kummel and Raup, 1965, pp 267-270). Various methods for obtaining cuticular samples (Abbott, 1950; Cridland and Williams, 1966; Chandrasekharam, 1972) were tried without success. Similar methods were attempted on the upper megafossil horizon as well as bulk maceration, but again with negative results.

Palynological Techniques - Attempts were made to recover microfossils from both the plant megafossil horizons and from the coaly shale lying between them. Recovery of microfossils in general requires three basic steps; breakdown of the matrix (either physically or chemically) to free the encased microfossils, removal of unwanted chemical residues (either inherent or created by the first step) and preparation of the cleaned, isolated microfossils for microscopic examination and photography. For the purposes of the remainder of the discussion, the term microfossils shall include two groups, (1) palynomorphs, including spores and pollen grains, and (2) other microfossils, including faunal remains (shell fragments, opercula, etc.), oogonia of *Chara* (*Gyrogonites*) and other algal remains. Components of the latter group are much less resistant to strong oxidants, and the matrices were therefore handled in a different fashion.

While slightly modified techniques were used in

attempting palynomorph recovery for each stratum, the only success was achieved on the coaly shale. Therefore, the methods used on it will be described in some detail, and unsuccessful modifications mentioned at its conclusion.

1. Coaly shale was broken into pea-sized pieces and a ten gram sample was weighed out. The sample was placed in a polyurethane beaker. The sample was then covered with 20% hydrochloric acid and allowed to stand for one hour to remove any carbonates.
2. After carbonate removal the sample was rinsed and covered with 52% hydrofluoric acid for a 24 hour period to remove silicates.
3. After thorough rinsing in distilled water and dilute hydrochloric acid the sample was covered with Schulz's reagent for the final oxidation of the remaining pieces of primarily carbonaceous material. For the particular sample, 2-3 hours was sufficient.
4. After rinsing to neutrality the material was placed in 2% sodium hydroxide. This step is critical, as the exines of the palynomorphs will begin to be etched if left too long in a basic solution. Therefore, every three minutes a sample was checked under the microscope, and as soon as grains could be observed free from the tarry residue from the Schulz's reaction, the material was diluted to neutrality. For the particular sample in question, six minutes proved adequate. It might be noted here that it is the opinion of some palynologists

(personal communications) that this length of time in a basic solution will completely dissolve some of the more delicate grains or change the ornamentation of more resistant ones. To guard against this possibility, a portion of a sample was removed and diluted after each minute, but later comparison with the six minute samples showed no observable difference.

5. The material was then wet-sieved through a series consisting of 300, 125, 63 and 45 micron mesh. The material collected on each sieve (and that passing through all of them) was then stored in distilled water made slightly acid with HCl to discourage water-mold growth.
6. For preparation of permanent slides the material was stained and mounted. A variety of methods were tried at this stage, but the optimum results were obtained as follows. Equal parts of a 1% solution of aqueous safranin and a 1% solution of Bismarck Brown were mixed and then diluted 1:100 with distilled water. Two drops of this stain were placed on a cover slip (60 x 22 mm proved easiest to handle) with one drop of the material (pH neutralized) containing the palynomorphs and one drop of polyvinyl alcohol (the exact percentage of the alcohol was not measured, but best results were obtained with a solution about the consistency of Karo syrup). These were mixed together and spread evenly across the cover slip. The cover slip was then placed on a warming tray to dry, after which it was mounted

with Permount on a glass slide.

In addition to the safranin-Bismarck Brown staining combination, the two components were tried separately. Basic fuchsin, which requires dehydration in a series of alcohol baths, was also tried. The safranin-Bismarck Brown combination gave the best results because it stained the grains in such a way that they showed the best detail when photographed. In addition it was noted that in many instances bisaccate grains subjected to this combination of stains absorbed the red safranin on their bladders and the yellow of the Bismarck Brown on their central bodies When photographed with a green filter this allowed for better differentiation of bladders. This was desirable as the relation of these to the central bodies of winged grains is an important taxonomic character

Other Microfossils - Preparation of material for retrieval of other microfossils necessitated omission of the use of the strong oxidizing agents used in the previous procedure. Two methods were therefore tried. In the first, the material was merely powdered and wet-sieved through the same mesh series. Samples from the two coarser meshes were then examined under a dissecting microscope for megaspores, *Chara* oogonia, etc. In the second method, material (about pea-sized chunks as in the initial procedure) was placed in a beaker of "Quaternary O", a detergent, and slowly boiled. This accomplished breakdown of the matrix without violent oxidation. The material was then rinsed, wet-sieved,

and searched in a similar manner. Neither of these methods yielded any results when tried with materials from all three layers.

Palynomorphs in Megafossil Layers - Modifications of the previously mentioned procedure were tried on samples from the two megafossil horizons. In the case of the volcanic tuff layer it was possible to treat samples of the unconsolidated bentonite without any initial breakdown procedures. A sample was thoroughly suspended in distilled water using a Waring blender. The resulting suspension was allowed to settle for two hours, after which the liquid portion, containing much of the very fine clay, was decanted and discarded. The remainder was suspended in a solution of zinc chloride having a specific gravity of 1.9 and allowed to separate. The floating layer, which contained the organic material was removed and treated in the same manner as the original procedure starting at step four. Unfortunately the final preparation yielded almost no palynomorphs.

The upper plant megafossil matrix was treated in a manner similar to the coaly shale, with the omission of step three (Schulz's reagent) which proved unnecessary. Here again the results were negative. A glance at the stratigraphy of the remainder of the outcrop (Text-Fig. 2) shows numerous other layers of coal and coaly shale. Cursory examinations of several of these indicated that some of them could well yield significant results, but they are not

included within the scope of this thesis.

K-Ar Analysis - Approximately 30 pounds of bentonite from the plant megafossil horizon were processed to obtain quantities of biotite and sanidine large enough for K-Ar analysis. The raw bentonite was thoroughly suspended in water using a Waring blender. The resulting slurry was repeatedly washed and decanted until the majority of the fine clay minerals were removed. The remaining coarser mineral portion (approximately 4 lbs.) was dried with acetone and dry-sieved through a 45 micron sieve. The fraction retained on the sieve was processed through a magnetic separator and the two fractions placed in appropriately labeled containers. At this stage the material was turned over to Professor H. Baadsgaard of the Department of Geology for final purification and analysis. Information on the theory and procedures for this final analysis may be obtained from Dalrymple and Lanphere (1969).

Living Materials - For general comparison of gross morphology of the fossil material with extant species, direct observation of herbarium material was generally satisfactory. For some taxodiaceous genera and a few angiosperm species venation and mode of attachment was somewhat obscured, and for these cases it proved desirable to clear, stain and mount specimens of the living material for comparison. For this comparison the procedure described by Chandrasekharam (1972, pp 16-17) was employed with a minor variation.

To correlate the microflora (pollen and spores) with species represented by the members of the megafloras, it proved desirable to prepare mounts of some palynomorphs of corresponding extant species. For this a small amount of the extant pollen (either from herbarium sheets or living greenhouse plants) was placed on a microscope slide with two drops of aniline oil and one drop of 0.01% crystal violet. This was gently heated until the stain was taken up by the pollen grains and the oil was clear. The slide was successively flooded with xylene and blotted until the oil was all replaced. The pollen was then covered with Permount and a coverslip, and the slides dried.

Statistical Analysis - To accurately determine the floristic composition of each plant megafossil horizon and to enable a suitable study of interspecific and intergeneric variation to be carried out, the mass collecting technique was employed in obtaining the material to be described. To insure the success of the first objective it is necessary to eliminate as much subjectivity in specimen collection as possible to obtain as truly random sample of the flora as possible. If this is done it is possible to obtain significant figures on the relative occurrence of the included species. However, the success of this method is dependent on the assumption that the fossils themselves are randomly deposited. Fossils contained in the fossiliferous siltstone layer gave no indication of negating this

generalization, and specimen counts and percentages are thus given and analyzed in the systematic section of this study. However, it became quickly evident in the course of collecting that the fossils contained in the volcanic tuff horizon were very selectively deposited, and thus the technique of purely random sampling of this horizon was abandoned early in the study.

The second objective, study of interspecific variation, does not depend on the randomness of the sample but rather on its thoroughness. To augment the fossil samples, as large a representation of extant material as feasible was studied for the relevant genera. These were analyzed for size, shape, phyllotaxy, and mode of attachment. The statistical results of these studies are presented in the appropriate sections of the systematics chapter.

The same two objectives may be applied to the statistical analysis of a microflora. The randomness may be obtained by counting a given number of fields randomly chosen for a given slide of fossil material. As the primary emphasis of the thesis is a study of the megafloras, no attempt was made to do a detailed study of the intertaxon variation of the palynomorphs. The relative frequencies of the taxa encountered are presented in the appropriate portion of the systematics chapter.

CHAPTER 4

SYSTEMATICS

Introduction - Within the outcrops of the Smoky Tower locality are at least three separate fossil floras, two containing megafossils and one yielding microfossils. Although there is a relationship existing between them which will be discussed in a later chapter, they are distinct lithologic units and will be treated as such. The megafloras will be treated in detail, while the microflora will be briefly described, listing and illustrating the genera and species found.

The taxonomy and nomenclature of compression floras has long presented many problems for investigators in that field. The very nature of the material leaves the investigator on the horns of a dilemma. On one hand there is the justifiable practice of identifying fossil fragments - sometimes only a single fragment - and assigning them names. The practice is justified by the concept that a positively identified specimen, even representing only a fragment of a plant organ, can be useful in making stratigraphic correlations. This approach was used most frequently in the first half of this century. It is well documented by workers such as Berry (1916, 1924, 1935), Hollick (1930, 1936), Knowlton (1902, 1922), and Bell (1949).

The other major approach tends to view the fossil

material as representing organs or fragments of organs of entire botanical entities and populations of entities in which the organisms are subject to interspecific variation. Proponents of this philosophy usually assign entities to taxa only when statistically significant numbers of specimens are available. They treat those with sparse representation as either probable members of a previously well documented taxon, or as an entity unsuitable for formal identification (designated as *Incertae sedis*). This philosophy has been the dominant one in recent years, and has been espoused by such workers as MacGinite (1969), Axelrod (1962, 1964), and Chandrasekharam (1972). Not all workers can be categorized in the preceding manner and several of the more recent major workers in systematic paleobotany have used an approach which combines certain features of both previously mentioned schools. These include Dorf (1942), Brown (1962), and Becker (1969).

This hybrid approach is based on the principle that the fossils represent organs of biological entities. However, it is recognized that stratigraphic value may still be placed on a fragment if it possesses recognizable characters, and thus such individual specimens may also be assigned names, even if their botanical affinities are in doubt.

In this dissertation the main principle of the latter approaches, that the fossils represent organs of biological entities and are thus subject to the variability such a definition implies, will be followed. However, it will be

modified with two other considerations. The first of these is the recognition of form and organ genera as set forth in the International Code of Botanical Nomenclature (Stafleu, 1972, Division II, Article 3). Such genera are recognized if the natural affinities of the fossil material remain in doubt. In accordance with this, entities represented by only one or few specimens, if well preserved and readily characterized, are assigned to appropriate taxa.

The second consideration involves the endings of generic names for fossil material. The trend among many paleobotanists has been to assign fossil material to genera of extant plants without any change in the generic name. The arguments presented in favor of this are (1) that a more natural classification[1] is possible, and (2) that all characteristics of the fossil material are already accounted for within the diagnosis of the extant genus, and thus a new name is unnecessary. It is the opinion of the author that these two arguments are not entirely valid, and that they do not justify the inclusion of fossil material in genera of extant plants without change in the generic name.

Regarding the first argument, the creation of a more natural classification, it is the author's position that in

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[1] As is lucidly pointed out by Davis and Heywood (1963, pp 8-9), "natural classification" may be interpreted as either phenetic naturalness or as phylogenetic naturalness. When used in this thesis natural classification shall imply phylogenetic relationships unless otherwise stated at the particular instance.

addition to trying to achieve phylogenetic naturalness in classification, one must also consider the usefulness and clarity of the system. It is perhaps understandable to adopt the system of using names of genera of extant plants for fossils when dealing with such genera as *Ginkgo* in which there is only one extant species. To many plant taxonomists *G. adiantoides* (Unger) Heer and *G. laramiensis* Ward will be readily recognizable as names belonging to extinct plants. However, with genera such as *Acer*, having 14 species in the northeastern United States alone (Fernald, 1950), only specific authorities would recognize *A. bolanderi* Lesquereux as a name designating a fossil species.

The second argument, that all characteristics of the fossil material are included within the diagnosis of the extant genus, is true as a simple statement of fact. However, except for a few unique cases, the fossil material (by virtue of its fragmentary nature and preservation) does not demonstrate many of the characters which are taxonomically important in the delimitation of the genus.

As an example, many angiosperms are identified (or keyed out in texts) on the basis of reproductive organs. The fact that a given fossil leaf, for example *Acer bolanderi*, is the same as leaves found in representatives of the genus of extant maples becomes less important when it is realized that no data are available on such characters as reproductive structures or xylotomy which might indicate the two are quite distinct taxonomically. Thus, the similarity

of a fossil leaf (or other plant organ) to an extant counterpart does not, indeed cannot, be taken as evidence that the entire extinct and extant organisms are identical (at the generic level). To do so denies the paleobotanically proven fact that different plant structures evolve at different rates in certain organisms and negates the possibility that the majority of the organs of a given plant may have evolved into generic uniqueness in a given number of million years while one organ remained unchanged. With this in mind it is apparent to this author that it is neither logical nor natural to place such a fossil within a genus of extant plants where many characteristics and organs are known. It would appear that this situation is an example of what was envisioned when provision was made for organ and form genera in the nomenclatorial code.

In keeping with the aforementioned philosophy, all new genera described in this thesis and thought to be closely allied to genera of extant plants will be given names with endings differing from those of the extant correlative. It may be argued that this policy, if uniformly adopted, would add greatly to the number of names in use, and thus add confusion to the already copious body of literature. This, however, seems to be less objectionable than the possible inaccuracy and lack of clarity incurred by inclusion of fossil material representing single plant organs within genera of extant plants representing entire organisms, or at least several organs of a single organism.

No specific classification will be used in the section dealing with the microflora. For the two megafloras, the system of Engler and Prantl as presented in Willis (1966) is used for angiosperms. Gymnosperms are classified according to Dallimore and Jackson (1966) and all other vascular plants are classified according to the system given by Smith (1955). Some deviation from these systems is inevitable, but instances of this will be discussed in the appropriate portions of the text.

Volcanic Tuff Flora

This flora is the lower (Text-Figs. 1, 2) and older of the two megafloras found at the Smoky Tower locality. It is predominantly coniferous in composition (greater than 75%), but exact percentages for individual taxa have not been presented for the reasons stated in the statistical portion of the preceding chapter. The remains appear to represent flo[illegible] that grew at different times. The evidence supports [illegible]onclusion that the fossil *Equisetum* found in the layer ([illegible] included in the systematic descriptions) grew after initial deposition of the volcanic ash, and succeeds the time when leaves of the coniferous genera were deposited.

Systematic List of the Flora - Numbers in brackets in the following list represent the total number of specimens from various sources used for the study.

Class: Equisetinae

Family: Equisetaceae

Equisetum arcticum Heer (107)

Class: Gymnospermae

Order: Ginkgoales

Ginkgo adiantoides (Unger) Heer (38)

Order: Coniferales

Family: Cupressaceae

Thujopposites interruptus (Newberry) nov. gen. et nov. comb. (92)

Family: Sciadopityaceae[1]

Sciadopitophyllum canadense Christophel

leaves attached (11)

leaves unattached (79)

Family: Taxodiaceae

Glyptostrobus nordenskioldii (Heer) Brown (437)

Metasequoia occidentalis (Newberry) Chaney (136)

Class: Angiospermae

Sub-class: Dicotyledonae

Family: Cercidiphyllaceae

Cercidiphyllum sp. (12)

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[1] Dallimore and Jackson (1966) do not recognize this family, but place *Sciadopitys* in the Taxodiaceae.

Family: Platanaceae

Platanus raynoldsii Newberry (20)

Family: Ulmaceae

Zelkova sp. (16)

Incertae sedis (32)

Class: Equisetinae

Family: Equisetaceae

Equisetum arcticum Heer (1866)

If frequency based on numbers of specimens were presented for this flora, *Equisetum* would prove to be by far the dominant member. Examination of the material points up two important facts: (1) only underground (i.e. rhizomatous and tuberous) material is present, and (2) this material, unlike other plant remains in the horizon, runs through the matrix at all angles and in all directions, in many cases piercing foliar remains of other genera (Fig. 89). These facts indicate that the growth of *Equisetum* was secondary to the deposition of the remaining flora and the volcanic ash itself. The presence of a layer of coal directly above the rhizomatous *Equisetum*-bearing bed tempts one to make a comparison with the stigmarian underclays found beneath the coal seams in Pennsylvanian age deposits.

Description - Recent authors (Brown, 1962; Graham, 1965; Becker, 1969) have recognized the possible interspecific variation in *Equisetum* and have placed together remains

which show some variability in either *Equisetum* sp. or into *E. arcticum* Heer. These investigators do not recognize the numerous species erected earlier by Hollick (1936), Lesquereaux (1883) and Bell (1949). The specimens represented at the Smoky Tower locality fit into the original description of *E. arcticum* Heer and the quantity of material allows the circumscription of the diagnosis to be expanded. The rhizomatous portions exhibit maximum diameters of 2.0 cm with the average being about 1.5 cm. The largest intact rhizome recovered (Fig. 11) is just over 49 cm in length and includes 4 nodes bearing tubers.

Tubers were found to average 3.8 cm in length, having an obovate shape with a distinctly constricted proximal attachment (Figs. 5, 7, 10). The average maximum diameter was found to be approximately 1.5 cm, while the greatest number observed attached to a single node was six. Numerous scars were observed on many specimens (Figs. 5, 8, 10) to a maximum of 14. Nodes bearing tubers often were shown to produce roots (Figs. 5, 8) in the same manner as extant species. Some smaller rhizomes with only roots at the nodes were also collected (Fig. 4). The larger rhizomes consistently exhibited ribbing (Figs. 5, 8, 10) and preserved nodal plates (Fig. 9) all showed evidence of having either 12 or 13 vascular bundles. In two specimens the internodal cross-section was seen (Fig. 6). In both cases 12 vallecular canals and thirteen partitions were observed.

In a monograph of the sub-genus *Hippochaete*, Hauke

(1963) discussed in great detail the taxonomically significant characters of the included species and also listed 12 characters which could be used in constructing a phylogeny of extant species. It is interesting to note that only two of these characteristics, axis size and rhizome surface (smooth vs. rough or ridged), could be applied to the fossil material. Even these characteristics are of little aid in interpreting the material, in that large axis size (a relative measurement) is considered primitive by Hauke while a ribbed rhizome is considered advanced. Thus it is impossible not only to make any phylogenetic interpretation from this type of material, but it is also obvious that the majority of characters considered taxonomically significant are not observable in compression fossils of this type. This combination of axis size and ribbing found in the fossil material would also tend to cast some doubt on their usage by Hauke in relation to phylogenetic interpretation of extant species.

Remarks - As noted earlier, all specimens observed fall within the limits of the diagnosis by Heer for *E. arcticum* and are similar to specimens figured and described by Bell (1949) and Becker (1969). Based on the internal structure exhibited by the Smoky Tower specimens it would be possible to emend the diagnosis. However, as the taxon has assumed the role of a good organ species representing a fairly large range of gross morphological features, there appears to be no advantage in increasing the specificity of the diagnosis.

FIGURES 4-11.

Figs. 4-11. *Equisetum arcticum* Heer from the tuff horizon.

Fig. 4. Specimen S1642 - small rhizome showing roots at the node. X 3

Fig. 5. Specimen P67.1.8 - a node showing one large attached tuber and numerous root and tuber scars. X 2

Fig. 6. Specimen S3164A - an internodal cross section of a rhizome, showing the probable pith and vallecular canals. X 3.5

Fig. 7. Specimen P67.1.33 - portion of a rhizome showing a node with two attached tubers; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 1.4

Fig. 8. Specimen S3108 - rhizome showing internodal ribbing and two attached tubers. X 2.5

Fig. 9. Specimen P67.1.81 - nodal plate showing probable ring of vascular bundles; deposited in the Alberta Provincial Museum and Archives collection. X 2.8

Fig. 10. Specimen S2894 - rhizome showing internodal ribbing and two attached tubers. X 1.4

Fig. 11. Specimen P67.1.1 - single rhizome showing several nodes and internodes with tubers attached at the nodes; deposited in the Alberta Provincial Museum and Archives collection. X 0.3

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As is shown by Hauke's criteria for determining species of *Equisetum*, the comparative values of *E. arcticum* in terms of intergeneric differences and comparisons with the modern flora are negligible. The value of the species therefore lies primarily in that it provides a basis for correlations with other fossil localities.

ORDER: GINKGOALES

Ginkgo adiantoides (Unger) Heer 1878

Description - Among the 38 specimens studied from the Smoky Tower locality, it was possible to observe almost all of the variations in leaf shape observed in *Ginkgo biloba* by Chamberlain (1935 - Fig. 206). Lobing varies from non-existant to deeply lobed (Figs. 12-15) and in general outline, from cuneate (Fig. 15) to approaching reniform, which is the commonest shape in the extant species. When present, petioles are seen to be well developed, almost equaling the length of the lamina in smaller specimens (Fig. 16) and almost twice that length in some more mature specimens (specimen S3409A - unfigured). Venation was also found to be consistent with that observable in the extant species. Parallel venation with open dichotomies (Fig. 17) was observed in all specimens in which venation is preserved.

Remarks - As with all other taxa (excluding *Equisetum*) found in the volcanic tuff stratum, those specimens found

in situ[1] were extremely localized in their lateral distribution (Text-Fig. 6). In one instance several leaves found in a single piece of tuff (Fig. 3) exhibit the varying degrees of polymorphism discussed earlier.

In recent years much speculation has been undertaken in regard to the evolution within the genus and the taxonomic variation. The observation has been made that the cuneate shape dominated in the Cretaceous specimens while the reniform shape first appeared in the Paleocene, although some specimens of this age and younger (including the extant *G. biloba*) still persisted in a cuneate variety (Brown, 1939, 1962). Brown summarized his feelings on the taxonomy of the fossil *Ginkgo* specimens with the following statement (1962, p. 47):

> "As the first well-developed reniform leaves of *Ginkgo* appear in the Paleocene, I favor restriction of *G. adiantoides* to the Cenozoic. This species, however, like *G. biloba*, may include leaves having the form of the Cretaceous *G. laramiensis* and the Jurassic *G. digitata*. When, therefore, these kinds only are found in a Paleocene or later collection, they can, nevertheless, be identified as *G. adiantoides*, on the presumption that they are such variants. Certainly less harm, if any, is done by this practice than, for example, to identify simple, undivided cuneate *Ginkgo* leaves, wherever found, whether in Mesozoic or Cenozoic strata, or even on the living tree, as *G. laramiensis*."

As observed by some earlier workers (Berry, 1935, Dorf, 1942), the supposed difference attributed to *G. laramiensis* is only observable where large suites of fossils are at

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[1] A large quantity of material, brought down by erosion and the original road construction is included in the study but not listed as *in situ*.

hand. However, the validity of the species *G. laramiensis* is not the central focal point of the issue. While most paleobotanists and taxonomists will agree that lumping all cuneate leaves from the Jurassic to the present in one species is absurd, it is equally unreasonable to separate Cretaceous and Paleocene specimens which are identical merely on their stratigraphic occurrence. Large numbers of plant species are found which span the Cretaceous-Tertiary boundary without change, and thus it does not appear to do "less harm" by assuming *Ginkgo* did not span this boundary than by assuming it did.

In an extensive study of the evolutionary trends in the genus *Ginkgo*, Tralau (1968) observed that some of the Cretaceous specimens in which cuticles were present could be shown to differ slightly from the Paleocene ones by the presence of papillae on the subsidiary cells around stomates. He also observed that one Eocene specimen differed from the extant forms in stomatal characters, while most other upper Cretaceous and Tertiary forms were well within the bounds of variability shown epidermally by *G. biloba*. An additional significant fact mentioned by Tralau was that the majority of specimens and taxa with affinities to *Ginkgo* from the Cretaceous and Tertiary did not have cuticles preserved, and thus it was impossible (excluding some lower Cretaceous specimens) to distinguish them satisfactorily.

Based on Tralau's study and on observations of specimens from various localities it is the opinion of this author that

FIGURES 12-17.

Figs. 12-17. *Ginkgo adiantoides* (Unger) Heer from the tuff horizon.

Fig. 12. Specimen S2738A - small leaf showing no lobing. X 2.2

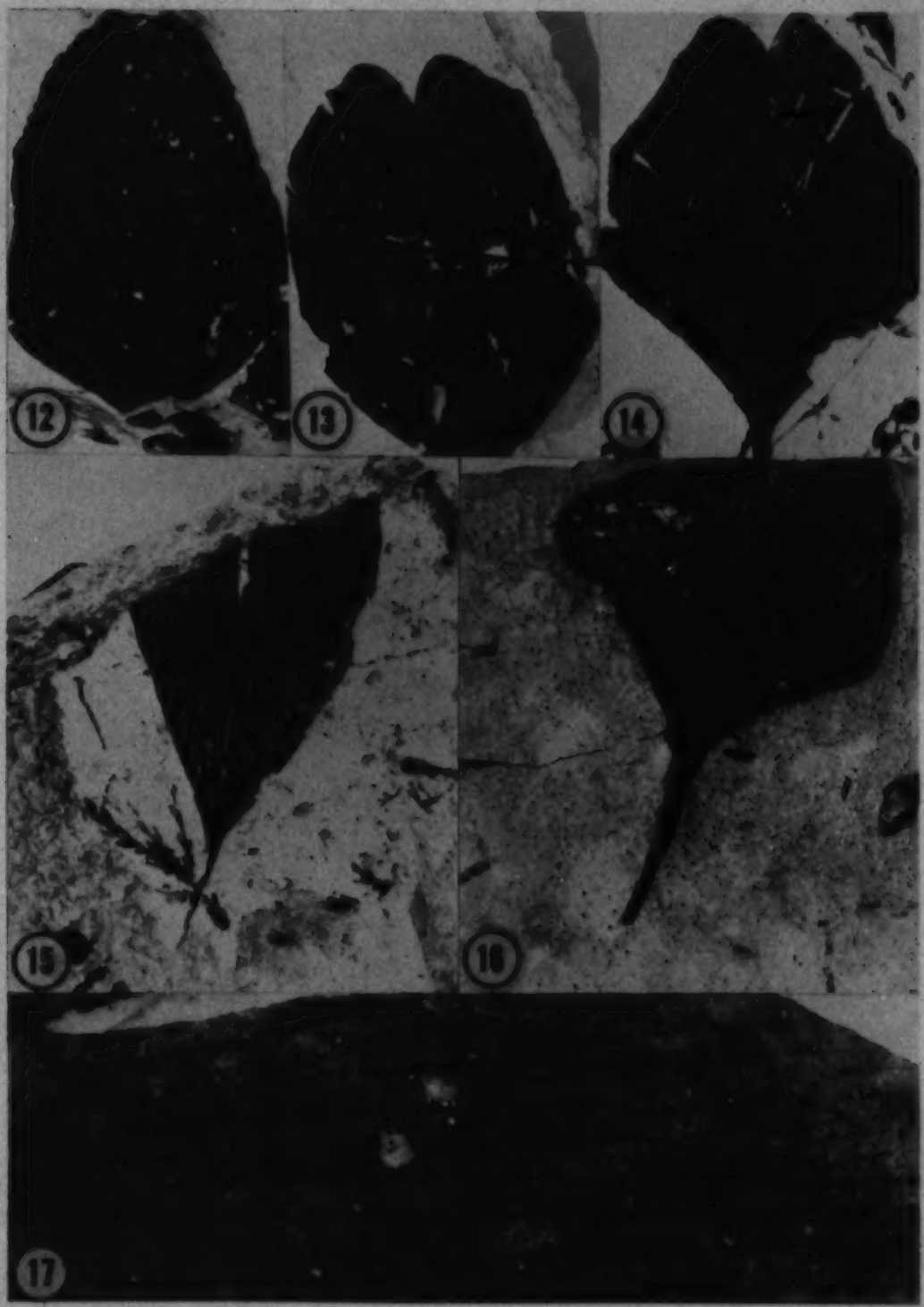
Fig. 13. Specimen S2738B - small leaf showing slight lobing. X 1.7

Fig. 14. Specimen S2733A - leaf showing slight lobing and a shape approaching reniform. X 1.4

Fig. 15. Specimen P67.1.142 - leaf showing moderate lobing and definite cuneate shape; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 1

Fig. 16. Specimen P67.1.79 - leaf showing a petiole of approximately the same length as the leaf lamina; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 2.1

Fig. 17. Specimen S1918A - portion of a leaf showing the dichotomizing veins near the leaf margin. X 8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unless the diagnosis is emended to include definite cuticular variants, the species *G. laramiensis* would be best placed in synonomy with *G. adiantoides* due to the lack of significant characters of a general nature that distinguish the two. The specimens from the Smoky Tower locality are definitely Tertiary, and thus assignable to *G. adiantoides* no matter whose taxonomic philosophy is followed. However, as a general principle, it would appear that more confusion might be caused by assigning noncuticularized, cuneate *Ginkgo* leaves from a locality 65-70 million years old to *G. laramiensis* because of their age than to assign them to *G. adiantoides* on the basis of their morphology.

ORDER: CONIFERALES

FAMILY: CUPRESSACEAE

Genus: *Thujopposites* gen. nov.

Diagnosis - Branchlets flat, linear, opposite, and deciduous; subtended by pairs of persistent, opposite cupressoid leaves. Leaves four-ranked, appressed, with laterals having acute apices and upper and lower ranked leaves being mucronate. Leaf tetrads show no indication of spiraling, with the midveins of the upper and lower ranked leaves forming continuous, straight rows along the branchlets. Larger axes naked with the exception of the opposite pairs of scale leaves subtending positions of dehisced branchlets.

Thujopposites interruptus (Newberry)

Christophel comb. nov.

Thuja interruptus Newb., 1868, Ann. N.Y. Lyc. Nat. Hist., Vol. IX, p. 42.

Libocedrus sabiniana Heer, 1871, p. 34.

Thuites interruptus (Newberry) Bell, 1949, p. 52.

Libocedrus interruptus (Newberry) Pabst, 1968.

Diagnosis - Branchlets flat, linear, opposite, and deciduous; subtended by pairs of persistent, opposite cupressoid leaves averaging 8-10 mm in length. Leaves four-ranked, and appressed. Lateral leaves averaging 6-9 mm in length with acute apices. Upper and lower ranked leaves mucronate, averaging 6-10 mm in length and 5-7 mm in width at the base. Heavy midrib prominent on upper and lower ranks of leaves giving the appearance of a continuous line along the branchlet (Fig. 22). Larger branches naked, excepting paired leaves subtending areas of dehisced branchlets (Fig. 19). Average distance between branchlets is 25-28 mm when measured on mature branches where dehiscence has already occurred.

Holotype - The same specimen as the basionym, *Thuja interrupta* Newberry.

Hypotypes - S-1820 (Figs. 21, 22) and S-3451A (Fig. 19) deposited in the paleobotanical collection, Department of Botany, University of Alberta, Edmonton.

Description and Discussion - The new genus and combination are based on *Thuja interrupta* Newberry which is the nomenclatorial basionym for the *comb. nov.* The original species diagnosis (as quoted in Newberry, 1898, pp 25-26) reads as follows:

> "Branchlets flat, narrow, linear, pinnate, opposite, except at the summit of the branch, somewhat remote, connected only by the slender woody axis on which the leaves of the branchlets are not decurrent; leaves in four rows appressed, those of the upper and lower ranks orbicular or obovate, shortly mucronate, lateral ones longer, subulate, terminating in awnlike points; larger branches naked or bearing closely appressed linear scalelike leaves."

The above diagnosis has been emended here to include the deciduous nature of the branchlets and some measurements of leaf size which are not inconsistent with those of the species listed in synonomy. While the original diagnosis stated that branches are not opposite at the apex, it appears that Newberry's observations were based on specimens where apical branching was obscured, due in some measure to the density of the branchlets in that region. In all specimens observed from the Smoky Tower locality, even ultimate branchlets are opposite (Fig. 18).

Pabst (1968) reviewed the material previously placed in *Thuja interrupta*, and based on additional material from the Chuckanut Formation in Washington, placed the entire complex in the genus *Libocedrus*. Her decision was based, in part, on a study of the extant incense cedar of California and Oregon and the Chilean cedar of South America. It is interesting to note that while Pabst considered both

of these species to belong to the genus *Libocedrus*, many other authors (Florin, 1963, and Dallimore and Jackson, 1966) considered them distinct enough to belong in separate genera (*Calocedrus* and *Austrocedrus* respectively).

The author had the opportunity to study Pabst's material while visiting the University of Berkeley, California, and reached the conclusion that the Chuckanut material was as similar to the extant genus *Thuja* as it was to any of the others just mentioned. The foliar specimens and the apparent reproductive structures can be definitely classed as cupressoid, but not positively placed with a genus of extant plants.

The decision to establish a new genus was based on the above-mentioned observations. The fact that Florin (1963) refused to separate the closely allied genera of the Cupressaceae in his consideration of their distribution in time and space also indicates the potential value of a new organ genus for this type of material. While the leaves most closely resemble *Thuja* in their size and shape, precedent has been set for the creation of a new genus based on opposite arrangement of vegetative units. An analogous situation existed in the Taxodiaceae with the creation of the genus *Metasequoia* Miki. Thus the new name indicates the similarity of the leaf size and shape to *Thuja* (particularly to *Thuja plicata* as can be seen in Figures 20 and 23), and also indicates the opposite nature of the branchlets not found in extant members of the genus. The generic ending

for the new name is in keeping with the principles stated in the opening pages of this chapter.

No reproductive structures assignable to the taxon have been found at the Smoky Tower locality. However, in a personal communication, Mr. H. Schorn, University of California, Berkeley, has described a specimen from the Tertiary of Washington which has vegetative remains definitely assignable to the taxon and also what appear to be female cones attached showing opposite arrangement of scales. Such evidence would add definite strength to the validity of the genus, and it is hoped that further study of the material can be made.

Chaney and Axelrod (1959) made a thorough study of the Miocene beds of the Columbia Plateau in which the Cupressaceae was well represented. Of the four genera discussed and figured by them, however, none shows evidence of opposite arrangement, and from this it can be deduced that either the genus *Thujopposites* did not extend that far geographically or that the genus had evolved or become extinct by that time. To the best of this author's knowledge, no reports of the genus are found in the literature of material younger than Paleogene age.

FIGURES 18-23.

Fig. 18. Specimen S1960A - *Thujopposites interruptus* (Newberry) comb. nov. showing the opposite pattern of branching extending to the apex of the axis. X 1.5

Fig. 19. Specimen S3451A - hypotype of *T. interruptus* showing the opposite pairs of leaves remaining on major axes after branchlet dehiscence. X 1.3

Fig. 20. Branch of extant *Thuja plicata* (red cedar) showing the alternate arrangement of branchlets and subtending scales after branchlet dehiscence. X 1.3

Fig. 21. Specimen S1820 - hypotype of *Thujopposites interruptus* showing the opposite arrangement of branches and leaves. X 1.5

Fig. 22. Specimen S1820 - enlarged view of Fig. 21 showing the decussate leaf arrangement and the almost continuous dark line formed by the midribs of facing leaves. X 3.2

Fig. 23. Enlarged view of Fig. 20 showing alternating branchlet arrangement and attenuated bases of the leaves on the major axis. X 4

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FAMILY: SCIADOPITYACEAE[1]

Sciadopitophyllum canadense Christophel[2]

Generic diagnosis - Foliar shoots bearing whorls of lanceolate leaves with a distinct dark line running the length of the leaf in the position of a midrib. Each whorl is subtended by a group of scale leaves also apparently arranged in a whorl. Lateral branches, when present, are short, having the appearance of a spur shoot, with whorls of the two types of leaves at the tip. Between groups of whorls other scale leaves occur in a loose spiral on longer shoots.

Species diagnosis - Foliar shoots bearing whorls of from 8-12 lanceolate leaves ranging 6-16 cm in length and 2-5 mm in width at the widest portion of the leaf. These whorls are subtended by a group of scale leaves ranging in length 1-3 mm. Near the shoot apex, whorls of leaves are spaced 6-11 mm apart. Lateral branches, when present, show a maximum length of 12 mm before production of the first set of leaf

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[1] Dallimore and Jackson, whose classification is being used here for conifers, do not agree with placing genera related to *Sciadopitys* in a separate family. However, various authors, including Arnoldi, Buchholz, and Florin have at various times supported separation of this group from the Taxodiaceae. For reasons stated later in the chapter, this viewpoint is supported by the author.

[2] Much of the descriptive material is either taken directly or paraphrased from the original article describing the genus (Christophel, 1973). However, as the taxon is based entirely on material from the volcanic tuff horizon of the Smoky Tower locality, much of that paper is included here for the sake of the completeness of the thesis. Text-Fig. 3 and Figs. 24-32 are taken directly from that paper, though are renumbered to fit the thesis sequence.

whorls. Spirally arranged scale leaves are placed 1-2 mm apart along the vertical axis. These scale leaves are the same size as those borne in apparent whorls below the long leaves.

Holotype - Specimen S3016 (Fig. 24) which is deposited in the paleobotanical collection, Department of Botany, University of Alberta, Edmonton.

Paratypes - Specimen S2890 (Fig. 28), specimen S2874B (Fig. 35), and specimen S3064B (Figs. 33, 34) which are deposited in the same paleobotanical collection as the holotype.

Description and Affinities - Prior to the publication of the diagnostic paper (Christophel, 1973) numerous detached leaves of *Sciadopitophyllum canadense* had been collected at the locality. Lack of cuticular material allowed speculation when considering the affinities of the material to include the podocarps, the pines, *Sciadopitys*, and even the sedges. Based on only the detached leaves, little thought was given to *Sciadopitys* affinities, because one of the obvious morphological features of this genus is the presence of bifurcate leaf tips, which is clearly absent in the fossil material (Fig. 29). Discovery of specimens showing attached leaves in the summer of 1971 suggested a strong relationship with *Sciadopitys*, and a comparative study with living and herbarium material was begun.

Needles from a forty-year-old herbarium sheet (Fig. 30)

showed not only a tendency for the bifurcate leaf tips to become obscure, but also for the stomatal groove to become considerably darkened, giving the impression of a single median vascular trace (Fig. 32). Although this was the oldest sheet examined, it is interesting to note that the number of obscured tips and the darkening of the stomatal furrow increased with the age of the herbarium sheet. Even living material showed a striking variety in apex morphology. For example, Fig. 31 (A) shows a young needle, Fig. 31 (B) a mature needle, and Fig. 31 (C) a dehisced needle approximately two weeks after abscission. Only in the mature, attached needle is the bifurcate tip an obvious characteristic.

A comparison of the fossil type specimen and a young shoot from a herbarium specimen of *Sciadopitys verticillata* shows an obvious similarity in their gross morphology (Figs. 24, 25). Close observation of their respective leaf attachments shows even strong similarities (1) in the spacing of the spirally arranged scale leaves on the main shoots, (2) in the apparent whorled nature of the long leaves and the subtending scale leaves, and (3) in the linear spacing between groups of leaf whorls (Figs. 26, 27). The brevity of this spacing is also significant in interpreting the apparent lateral "short shoots" encountered in some specimens (Figs. 28, 35, 36).

Young lateral shoots of both fossil and extant specimens may have the appearance of spur shoots such as those

found in the genera *Ginkgo* and *Larix*. They differ from true spur shoots, however, in that they maintain successive whorls of leaves as the shoot increases in length and they display internodal growth of the same magnitude as main shoots. Thus, although the specimens in Fig. 28, Fig. 35, and Fig. 36 appear to have spur shoots, these would probably all have the appearance of the shoot shown in Fig. 24 if they had matured. The whorl of leaves directly subtending a new lateral shoot has the tendency in the extant species to abscise soon after lateral shoot production. This tendency could not only account for the absence of leaf whorls on the main axis of the specimen in Fig. 28, but could also explain the large quantities of detached leaves found at the locality. It is true that in the extant *Sciadopitys* the branch buds produced in the axils of scale leaves develop at a much more acute angle than illustrated by *Sciadopitophyllum*, the average angle in the former being 38-48 degrees, while in the latter 75-85 degrees. It is also worth noting that the extant species shows a marked tendency to retain the flange of scale leaves below the newly developed bud, while this is not true in the fossil material. However, though both of these points may be used to justify placing the fossil material in a genus other than *Sciadopitys*, they do not appear critical enough to negate the possibility of a close relationship to *Sciadopitys*.

One specimen (Figs. 33, 34) was mentioned in the original paper (Christophel, 1973) because of its variation

in leaf position. Unlike the extant genus, and all other specimens of *Sciadopitophyllum* collected to date, this specimen shows long leaves attached singly along the major axis in an apparent spiral fashion. In addition, the specimen shows the typical whorled arrangement (Fig. 33, letter W) of long leaves at either a node or on a short shoot. The letter B in Fig. 34 shows an apparent short shoot bud, which in this case is also subtended by a long needle instead of either a flange or single scale leaf as found in the other fossil material. This specimen is then open to three possible interpretations. It may be interpreted (1) to represent a unique genetic variant within the population, (2) to indicate a possible ancestral character which has been lost, repressed, or modified in the extant genus, or (3) as giving evidence that the fossil material is not as closely related to the genus *Sciadopitys* as was postulated in the original description of the genus.

As only one specimen showing these somewhat different characteristics was recovered, all three interpretations must be seriously considered. However, the third possibility seems least likely, in that the characteristics by which this specimen differs from the other material of *Sciadopitophyllum* are not great enough to taxonomically isolate it from them.

The genus *Sciadopitytes* Goeppert and Menge (1883) was used to describe isolated leaves which showed a *Sciadopitys*-like epidermal pattern. All species of this genus reviewed

by Florin (1922) were also isolated leaves from which epidermal structures were obtained and described. The new material of *Sciadopitophyllum* differs from that described previously for *Sciadopitytes* in that (1) leaves are found attached to axes, (2) no bifurcate tips are present, and (3) cuticular remains are completely lacking. For these reasons, it is difficult to justify combining *Sciadopitophyllum* and *Sciadopitytes*. In recent years many paleobotanists have erected new species within the genus *Sciadopitys* for remains found in late Cretaceous or younger strata. Many of these, such as *S. marcodurensis* Weyland, Kilpper, and Berendt (1967), are also based on similar epidermal structures and are thus more justifiably placed in the genus. The obvious similarities of both *Sciadopitophyllum* and *Sciadopitytes* to the extant *Sciadopitys*, however, leave little doubt about the close relationships of the three genera.

In the original paper (Christophel, 1973) note was made of a possible association between *Cryptomerites* and *Sciadopitophyllum* at the type locality. Since that time, however, an extensive study of the supposed *Cryptomerites* has shown it to be the cryptomerioid foliage of *Glyptostrobus*. *Glyptostrobus*, often found in the fossil record in association with *Cercidiphyllum* and *Metasequoia*, is a monotypic genus restricted to the Chinese coast and thus a member of the relict Sino-Japanese flora which also includes *Sciadopitys* and *Cryptomeria*.

Based on morphological similarities discussed above and on ecological associations, it appears there is sufficient evidence to place *Sciadopitophyllum* in the Sciadopityaceae which already contains *Sciadopitytes* and *Sciadopitys*. Placing *Sciadopitophyllum* on a distribution map with the two latter genera (Text-Fig. 3, *Sciadopitophyllum* indicated by a solid triangle) indicates a more holarctic distribution for the family from the Cretaceous on. This might be expected from a study of its ecological and floristic associates.

Characteristics of the Family - Since the extant species *Sciadopitys verticillata* Siebold and Zuccarini (1841) was described, its relationship in regard to other conifers has been in question. In his classic work on cuticle analysis Florin (1931) showed both in stomatal distribution and structure that *Sciadopitys* was distinctly different from other members of the Taxodiaceae, and proposed that it might be wise to separate it into a distinct family. However, 32 years later (1963) in his equally classic work on conifer distribution he included them in the Taxodiaceae with hardly a comment. Pilger, in Engler and Prantl (1926) circumvented the problem by placing the genus in a separate subfamily (the Sciadopitinae) within the Taxodiaceae. Buchholz (1931) discussed suspensor development in the genus and also came to the conclusion that it differs significantly from other taxodiaceous members. More recent work on its embryology (Doyle and Brennan, 1971) states this difference succinctly:

"In practically all the examples already referred to

> [Taxodiaceae] the occurrence of cleavage has been associated with embryological advance. *Sciadopitys* adds to its special characters by being a complete exception to this general condition. The development of the proembryo closely resembles that of the simplest podocarps such as *Podocarpus andinus*. There are five post-fertilization mitoses before first membrane formation followed by the usual internal mitosis affecting commonly all the nuclei (Tahara, 1937). In the mature proembryo the E group contains many cells, up to 20 or more, and is multistoried and tapering. This represents quite a primitive embryogeny. Nevertheless, not only is cleavage present (Buchholz, 1931) but it is present in an advanced condition showing a 'primary suspensor' stage as in one type in the Taxodiaceae."

Recent work on guard-cell morphology in the Taxodiaceae (Boulter, 1969) at both the light and scanning electron microscope level shows that *Sciadopitys* also differs from all other taxodiaceous genera in the lignification of the guard cells as well as in general stomatal structure.

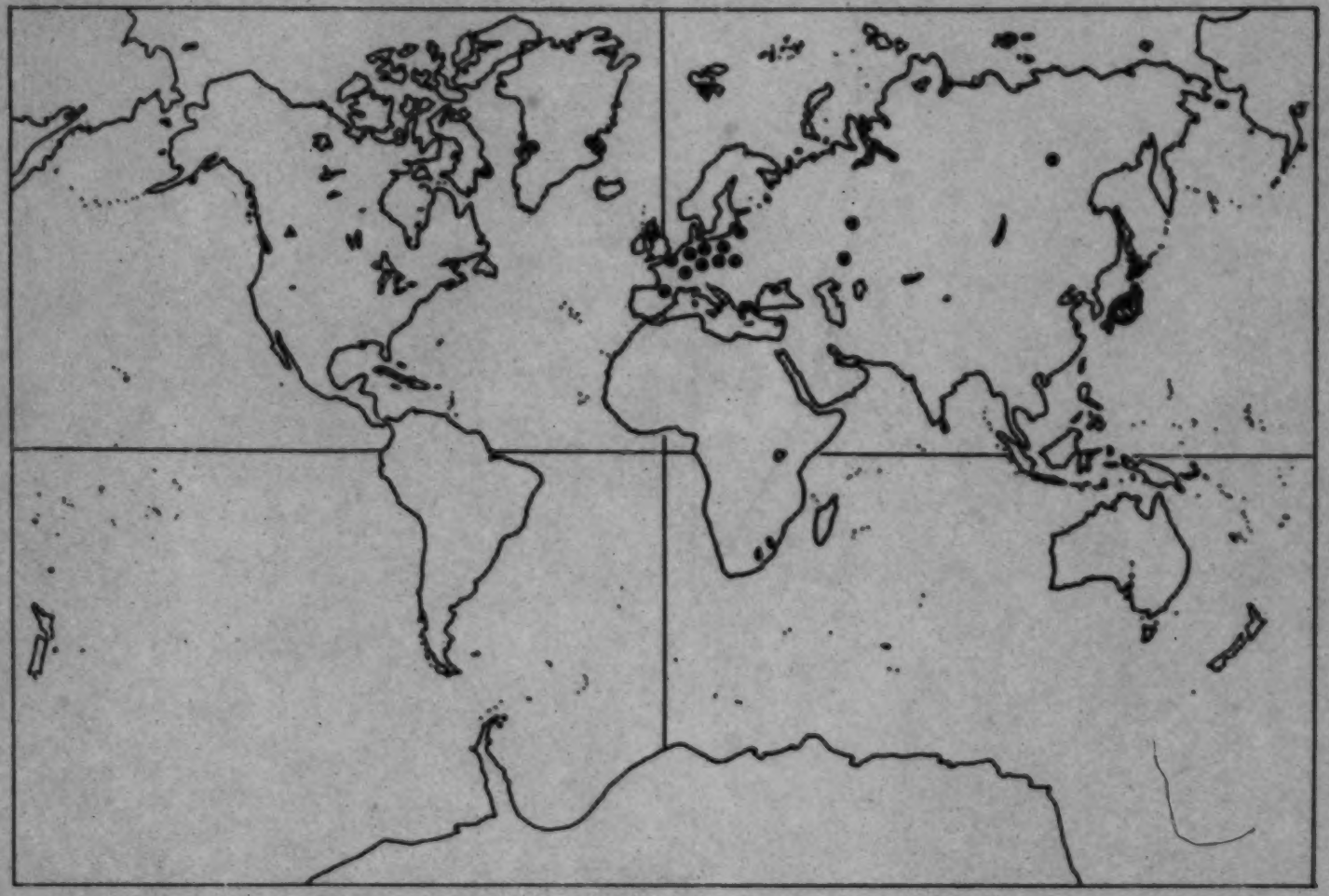
The general morphology of the vegetative portions of the plant has been discussed earlier, and the striking differences with the other taxodiaceous genera can be seen from this. In particular, the long leaves, thought by many to represent a short shoot or the lateral fusion of two simple needles, have been ontogenetically examined by Roth (1962) and shown to represent a unique form of meristematic growth which shows no indication that the double vasculature indeed represents the lateral fusion of separate simple leaves. She does not, however, rule out the possibility of the leaf representing a modified shoot.

Greguss (1955) makes note of the fact that, xylotomically, the genus is almost identical to members of the Podocarpaceae rather than the Taxodiaceae. This is shown most

dramatically in the crossfield pitting, where the diagnostic taxodioid form of pit is absent in *Sciadopitys*, its place being taken by a single large pit extending across the field as in *Phyllocladus*. Greguss escapes taxonomic complexities, however, by including the genus in both the Taxodiaceae and the Podocarpaceae in his systematic key.

The pollen grain with a thin exine and typical germinal papilla (*Taxodium*, *Cryptomeria*, *Athrotaxus*, *Sequoia*, *Metasequoia*) is absent in *Sciadopitys*. The latter has a spheroid to ovoid grain with a heavily sculptured exine. Thus, in most of the characteristics which may be considered taxonomically significant, *Sciadopitys* varies distinctly from the taxodiaceous type.

Despite this large volume of evidence, modern taxonomists persist in including the genus in the Taxodiaceae. Lawrence (1966) places it there with a footnote to the effect that there is some difference of opinion. Dallimore and Jackson (1966) do not even mention the possibility of separation into another family. In the opinion of the author, the evidence of the generic uniqueness is overwhelming, and a separate family, containing the genera *Sciadopitys*, *Sciadopitytes*, and *Sciadopitophyllum* is not only justified, but necessary if any credence is to be given to current taxonomic criteria.



TEXT-FIGURE 3. Distribution of the Sciadopitaceae in time and space. Hashed lines indicate distribution of extant *Sciadopitys*; solid circles indicate distribution of the family in the past; the solid triangle indicates the location of *Sciadopitophyllum canadense*.

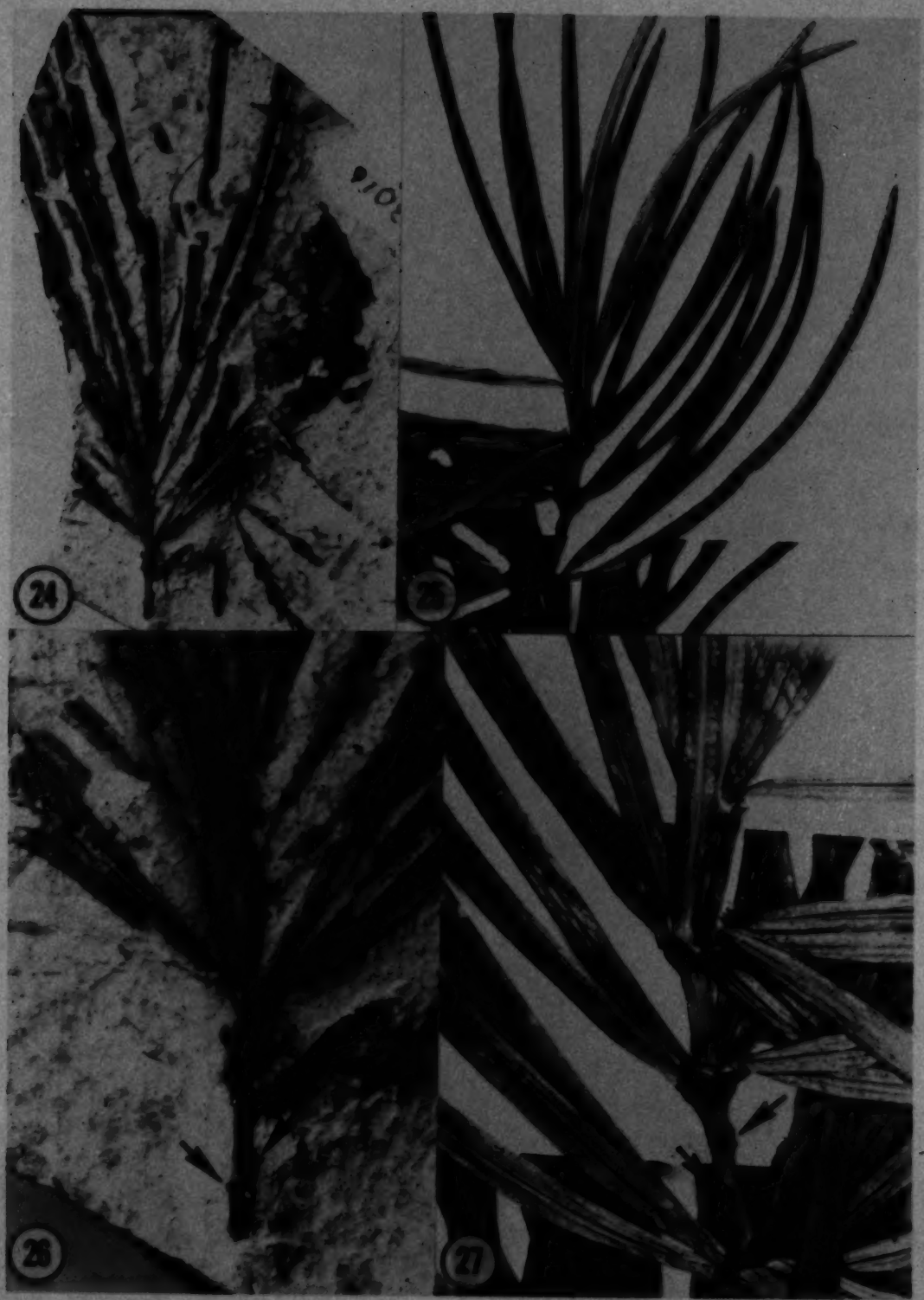
FIGURES 24-27.

Fig. 24. Specimen S3016 - holotype of *Sciadopitophyllum canadense* Christophel showing a young shoot with three whorls of long leaves, each subtended by a group of scale leaves. X 0.75

Fig. 25. A young shoot of *Sciadopitys verticillata* from herbarium sheet #A10452 of the Arnold Arboretum, Harvard University. Three whorls of long leaves are shown. X 1

Fig. 26. Specimen S3016 - an enlarged view of Fig. 24 showing the attachment of the leaf whorls. Arrows indicate loosely spiraled scale leaves. X 2

Fig. 27. An enlarged view of Fig. 25 showing the attachment of leaves. Arrows indicate loosely spiraled scale leaves. X 2


24
25
26
27

FIGURES 28-32.

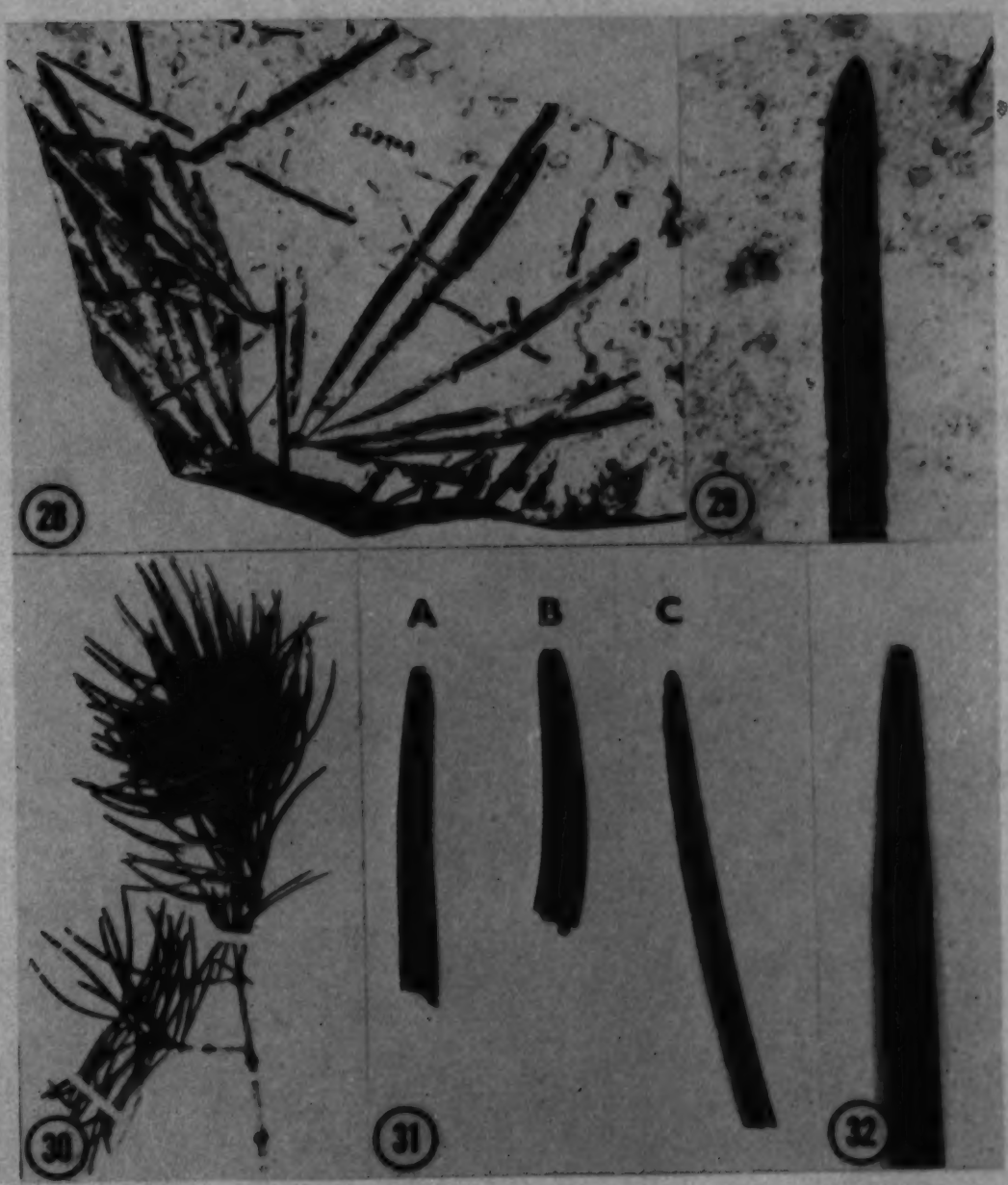
Fig. 28. Specimen S2890A - paratype of *Sciadopitophyllum canadense* showing two young shoots on alternate sides of the axis; also shows leaf attachment and a central bud. X 0.5

Fig. 29. Specimen S1645 - shows an enlarged leaf apex of *S. canadense*; a dark carbonized line runs the length of the needle and is comparable to the stomatal furrow position of *Sciadopitys verticillata*. X 2.5

Fig. 30. Herbarium sheet #10452 from the Arnold Arboretum; collected in 1933; shows a main branch and two lateral branches. X 0.25

Fig. 31. Leaf apices of *Sciadopitys verticillata* showing (A) the tip of a young leaf with little bifurcation visible, (B) the tip of a mature leaf showing pronounced bifurcation, and (C) the tip of a detached leaf (two weeks after abscission) showing no noticeable bifurcation and a definite dark midline. X 2

Fig. 32. Enlarged leaf apex of *S. verticillata* from Arnold Arboretum sheet #10452, showing no trace of a bifurcate tip and a pronounced blackened midline. X 2


28
29
30
A
B
C
31
32

FIGURES 33-36.

Figs. 33-36. *Sciadopitophyllum canadense* Christophel

Fig. 33. Specimen S3064B - paratype of *S. canadense* with a portion of axis showing whorls of long leaves (letter W) and also long leaves spiraled along the main axis. X 1

Fig. 34. Specimen S3064B - higher magnification of Fig. 33 showing a lateral bud (letter B) and spiraled long leaves. X 2

Fig. 35. Specimen S2874B - portion of an axis bearing a lateral shoot with a whorl of long leaves; a scale leaf appears opposite the lateral shoot. X 1.2

Fig. 36. Specimen S3013B - lateral branch showing apparent whorled attachment of the long leaves. X 3.1

W
33
34
35
36

FAMILY: TAXODIACEAE

Metasequoia occidentalis (Newberry) Chaney

In 1951 Chaney undertook a thorough revision of certain genera of taxodiaceous plants, with the major emphasis being placed on a comparison with the relatively newly discovered genus *Metasequoia*. In this discussion he designated two new combinations within the genus, *M. occidentalis* and *M. cuneata*. The former was considered to be a primarily Tertiary species, while the latter was primarily Cretaceous. The material from the Smoky Tower locality, somewhat intermediate in its morphology, is assigned to *M. occidentalis* for reasons stated later in the text.

A total of 136 specimens was studied from the Smoky Tower locality. Many of these, as with most other genera, were found to have a restricted lateral distribution in the tuff layer. This distribution is discussed in Chapter 5. No reproductive structures were found. Thus the structures used for species identifications were leaves attached to branches. Seventy-five specimens were measured and studied for statistical comparison.

This study showed that the average deciduous shoot[1]

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[1] A deciduous shoot is defined for this study as being one which consists of a single axis and shows no evidence of branching. In most instances this term may be equated with the term "short shoot" used by many authors. In a thorough morphological study it was pointed out by Böcher (1964) that "long shoot" and "short shoot" were not descriptive terms (in relation to *Metasequoia glyptostroboides*), but rather developmental ones. Thus they are not really appropriate in a discussion of fossil material, and deciduous shoot has been chosen as a more descriptive term.

contains 10-24 pairs of opposite to subopposite leaves. The average number is 14 pairs. Maximum needle length is 20 mm with the average being 8 mm. Maximum needle width is 3 mm with the average being 1.1 mm. The average L/W ratio proved to be just over 6:1, and the average axillary leaf angle was shown to be 68 degrees. A random sample of 200 needles was examined for their apical configurations. Of these 78 showed no well defined apex while 82 showed a definite mucronate tip, and 40 possessed what appeared to be complete tips but lacked mucra.

Based on terms used in the literature for the description of *Metasequoia* foliage three categories, ovate, obovate, and linear were chosen. When classification according to these categories was attempted, it was determined that 39 could not be adequately placed in any of the three categories, 76 would be classed as obovate, 54 as linear, and 31 as ovate.

In addition to the quantitative measurements, certain qualitative observations were also made. As may be seen in Fig. 39, the general shape displayed by the branches and leaves of a given specimen may be characterized as blunt. This configuration is probably related to the L/W ratio of the leaves and the leaf shape. Because it is difficult to describe, the difference in shape may be best shown by a comparison with other fossil specimens (Figs. 37, 38) and a specimen of the extant species, *M. glyptostroboides* (Fig. 40). Additional features exhibited by the Smoky Tower

material included the twisted nature of the petiole typical of the genus (Fig. 49), bulbous clusters of scale leaves at the base of deciduous shoots (Fig. 42), and persistent leaves subtending branches (Fig. 39).

Discussion - In a study of Chaney's 1951 paper, two observations regarding *Metasequoia* are apparent. The first is that fossil specimens belonging to this genus are readily distinguishable from those of other taxodiaceous genera. This subject will be dealt with more fully at the conclusion of the description of the family. The second observation is that there are two distinct fossil species of *Metasequoia* in North America, and that they have well-defined characteristics by which they can be distinguished. Doubt has been cast on this conclusion by other workers (Chandrasekharam, 1972), and it is the opinion of the author that reexamination of the material used by Chaney as well as that from Genesee and the Smoky Tower locality indicate that only one species is present.

In reference to the difference between *Metasequoia occidentalis* and *M. cuneata*, Chaney (1951, pp 229-230) stated the following:

> "Nowhere as common as *M. occidentalis*, its [*M. cuneata*] characters are less fully known; well preserved foliage may be distinguished from that of Tertiary species by the obovate shape of many of the needles; most shoots I have studied have fewer needles than those of *M. occidentalis*, and their divergence from the stem is less commonly at or near right angles."

Bell (1957) emended Chaney's diagnosis for *M. cuneata* and in a discussion which followed listed the following four

criteria (p. 31) by which this species may be distinguished from *M. occidentalis*:

> "However, the writer considers that *M. cuneata* differs from *M. occidentalis* in the following characters: (1) the short shoots were much less freely deciduous; (2) present lack of evidence for scale-like leaves at the base of the short shoots, similar to those so commonly found in *M. occidentalis*; (3) the leaves of *M. cuneata* in the axils of which the short shoots occur are generally persistent; (4) the leaves of long shoots are commonly curved somewhat backwards giving the foliage a more lax appearance than that of *M. occidentalis*,...."

If these differences are examined in light of the Smoky Tower material, some striking inadequacies in their diagnostic characteristics become apparent. With respect to needle shape, in his description of *M. occidentalis* (pp 226-227) Chaney states: "Leaves linear, of nearly the same width throughout...", while in his description of *M. cuneata* (p. 229) he states: "Leaves typically slender-oblanceolate,...". The Smoky Tower material shows 38% of the needles oblanceolate (though not necessarily slender) and 27% linear, thus making it impossible to use leaf shape as a criterion.

In relation to number of pairs of leaves per deciduous shoot, Chaney states that *M. occidentalis* has 20 or more while *M. cuneata* possesses 15-20. Smoky Tower *Metasequoia* shows 12-24, thus making this criterion somewhat questionable. Chaney's final characteristic is that the Cretaceous species, *M. cuneata*, has a lower angle of leaf divergence. By this criterion the Smoky Tower *Metasequoia* would be classed as *M. cuneata* with its average angle of 68 degrees. It is interesting to note, that in his discussion Chaney

indicates that this angle is a point of difference between *M. cuneata* and *M. occidentalis*. However, in the species diagnoses Chaney uses identical phraseology to describe the angle of divergence for each of the two species.

Looking at the first of Bell's criteria we immediately run into difficulties. The degree to which a plant is deciduous is not a character which may be readily used taxonomically. It is much more a function of the environment, as has been frequently observed by the author on specimens of *M. glyptostroboides* growing in various conditions in the greenhouses at the University of Alberta. A striking example of this feature was observed by the author on a trip to the campus of the University of California, Berkeley, in December of 1972. At this time the Bay area experienced the most severe frost it had known in 40-50 years. Within the space of three days, one particular *Metasequoia* not only lost all of its deciduous shoots, but each of these dropped all of its needles at the same time. Thus, a paleobotanist discovering the remains of *Metasequoia* from this particular area and season would call the species extremely "freely deciduous".

Bell's second criterion has been successfully refuted by Chandrasekharam (1972, p. 45) based on Genesee material. The Smoky Tower material definitely shows the presence of basal scale leaves as well, but preserved reasonably in only about 30% of the specimens. Thus it is not a character upon which ready reliance may be placed. Bell's third criterion

is again more closely environmental than taxonomic. Even if considered a good taxonomic character, it may be seen that both material from Genesee and Smoky Tower have persistent subtending leaves (Figs. 37, 39).

The fourth and final criterion used by Bell is the laxness of the needles of the long shoots. As may be seen in Fig. 49, the needles of the long shoots of the Smoky Tower material bend back to a certain extent, but the degree of laxness is subjective. In fairness to Bell it may be said that the specimens illustrated in his 1957 paper as *M. cuneata* do indeed recurve and have a definite lax appearance. However, the inclusion of these specimens in the genus *Metasequoia* is very doubtful and tends to eliminate this feature as a diagnostic characteristic for *Metasequoia*.

Based on the preceding discussion of the Smoky Tower specimens of *Metasequoia* and their comparison to the species characteristics given by Chaney and Bell, one of three possible hypotheses may be made. (1) Because the degree of similarity to *M. cuneata* is higher, the Smoky Tower material should be regarded as a Paleocene record of that species. (2) Because there is a definite degree of overlap in characteristics between the Smoky Tower specimens and Chaney's two species, the Smoky Tower material could well represent an intermediate species, or (3) finally, if the intermediate nature of the material supports the hypothesis that the basis for separation of *Metasequoia cuneata* and

M. occidentalis is not valid, then one or both of these species is not acceptable.

Using solely the descriptions and characteristics stated by Chaney and Bell, it would appear that although a majority of their characters favor placement in *M. cuneata*, the preponderance of evidence supports the view that the Smoky Tower material is indeed intermediate. To evaluate the second and third hypotheses, however, it is necessary to examine the specimens upon which the species are based.

In making the new combination, *Metasequoia occidentalis*, Chaney gave abundant evidence for its similarity to the living species. A comparison of Figs. 38, 40 and also of Figs. 47, 48 serve to illustrate this point well. It is the description of *M. cuneata* and the specimens that are included in the species that produce taxonomic problems. In the following discussion it should be emphasized that every specimen listed in synonomy by Chaney and later by Bell has not been examined as a part of this study. Only the material figured by the two authors will be critically discussed. This decision is based on the assumption that the authors considered the specimens they figured to be typical of the species.

Chaney illustrated six specimens (1951, p. 260, Plate 11, Figs. 1-6) to represent the characteristics of his new combination, *M. cuneata*. Using the two characters of leaf base and mode of attachment which these specimens show, Chaney placed them in his new combination (Chaney, 1951,

Plate 11, Figs. 5,3). Previously these specimens from Point of the Rocks, Wyoming, were called *Sequoia brevifolia* by Knowlton. For the following reasons they are more appropriately left in the genus *Sequoia* than placed in *Metasequoia*. In both specimens the leaf bases do not narrow appreciably to form a distinct petiole. They do not bend obliquely to the base of the next leaf, and at best they are subopposite, rather than distinctly decussate. The same general statement may be made for the specimen Chaney figured as #2 from the same locality. The specimen figured as Plate 11, #6 is not clear enough to make a definitive decision about its characteristics. The author did not have other specimens from Marmarth, North Dakota, from which to draw conclusions. The specimens figured in Plate 11, Figs. 1, 4 are the only ones which may be assigned to the genus *Metasequoia* with any degree of confidence. A comparison of these with Figs. 43, 45, 46, and 49 of this thesis will show that they fall well within the limits of either *M. occidentalis* or *M. glyptostroboides*. Thus none of the specimens figured by Chaney for his new combination, *Metasequoia cuneata*, give substantial evidence justifying the new combination.

There are nine specimens figured by Bell (1957) to support his emended diagnosis for *M. cuneata* (Plate XI, Figs. 3, 5, 6; Plate XII, Figs. 1-3; Plate XIII, Fig. 2; Plate XVII, Figs. 1, 7). As with many of the specimens figured by Chaney, the major problem here is justifying their

inclusion in the genus *Metasequoia*, let alone their assignment to the emended species, *M. cuneata*. Of all those specimens figured, only the one illustrated by Plate XVII, Fig. 1 can be placed with confidence in the genus *Metasequoia*. This is based on the observable opposite nature of the leaves and the oblique orientation of the leaf base. It is to Bell's credit that he eliminated much of the synonomy listed by Chaney, replacing these specimens in the genus *Sequoia*. Unfortunately, Bell makes no mention of the number of specimens studied, and it is impossible to determine the significance of the one *Metasequoia*-like specimen figured.

Based on the characteristics of the genus *Metasequoia* espoused by Chaney and Bell, it is possible to include only the specimens shown by Chaney (1951, Plate 11, Figs. 1, 4), the specimen shown by Bell (1957, Plate XVII, Fig. 1), and the one shown by Dorf (1938, Plate 1, Fig. 10 - *Sequoia nordenskioldii*) and possibly Dorf (1942, Plate 6, Figs. 4-11 - *Sequoia dakotensis*) within the genus.[1] Considering the wide variation shown in leaf and shoot morphology by the extant species *M. glyptostroboides* (Figs. 40, 45, 46, 47, all of the same plant) and by *M. occidentalis* (Figs. 41-44), it seems unreasonable to establish a new species for these few isolated specimens. Careful examination of the *Metasequoia* found at the Smoky Tower locality (Paleocene) shows that the description for *Metasequoia occidentalis* (Newberry) Chaney is not sufficiently broad to encompass the

[1] The specimen in Fig. 44 is Cretaceous, and figured by Dorf (1942, Plate 6, Fig. 6) as *Sequoia dakotensis*.

characteristics shown by all *Metasequoia* fossil remains. Therefore it is proposed that the diagnosis of *M. occidentalis* be emended to include this material, and that the few specimens described as *M. cuneata* which have been shown to be within the limits of the emended specific diagnosis be placed in synonomy.

Metasequoia occidentalis (Newberry) Chaney

Sequoia nordenskioldi(i) Heer, Dorf, 1938, Carn. Inst. Wash. Publ. 508, Plate 1, Fig. 10.

? *Sequoia dakotensis* Brown, Dorf, 1942, Carn. Inst. Wash. 508, Pt. II, Plate 6, Figs. 4-11.

Metasequoia cuneata (Newberry) Chaney, 1951, Amer. Phil. Soc. Trans. 40, pt. 3, Plate 11, Figs. 1,4.

? *Parataxodium wigginsii* Arnold and Lowther, 1955, Amer. J. Bot. 42: 522-528. Figs. 1-12.[1]

Metasequoia cuneata (Newberry) Chaney pars, Bell, 1957, Geol. Surv. Can., Memoir 293, Plate 17, Fig. 1.

Sequoia occidentalis (Newberry) Weide, 1962, Feddes Repert. 66(3): 159-192. Plates 1-7.[2]

Original Description - (Newberry, 1863, p. 516 for *Taxodium occidentale*)

"Branchlets terete, leaves numerous, crowded, generally opposite, sessile, or very short-petioled, one-nerved,

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[1]This taxon is placed in synonomy with some hesitation (thus the preceding question mark). The authors of the paper do not mention the institution at which the type material is stored and the decision to place it in synonomy is based on the figures in the paper and their description. An attempt is being made to locate the type material, and after doing this a reevaluation of the position of the taxon will be made.

[2]A discussion of the reasons for placing this taxon in synonomy may be found in Becker (1969, p. 66). The nominal paper is listed in the bibliography under Schwarz and Weide.

flat, rounded at both ends."

New Combination Description - (Chaney, 1951, pp 226-227, *Metasequoia occidentalis*)

"FOLIAGE SHOOTS bearing monomorphic, acicular leaves except at base where they form a stout, scaly tuft; of two types, long shoots which are persistent and develop into branches, and short shoots which are deciduous. LONG SHOOTS bearing needles up to 2.4 cm. long and 2 mm. broad; needles decussately attached and rotated into flat sprays prior to the development of short shoots in their axils, at which stage they show a return toward diametrically opposed position, and become widely spaced as the shoot lengthens and short shoots develop; not all pairs of leaves on long shoots have developed; if one short shoot of a pair fails to develop or is shed, a long shoot needle may persist on the stem opposite the short shoot which has developed; subtending needles commonly deciduous during or after short shoot growth. SHORT SHOOTS slender, straight or curving, up to 6 cm. long, bearing at maturity 20 or more closely spaced pairs of leaves, decussately attached but always rotated into distichous position except at the tip of growing shoots, longest at middle of shoot and gradually shortening to form a rounded apex; commonly shed separately. LEAVES linear of nearly the same width throughout, abruptly rounded at base and narrowed to a short petiole, bluntly rounded at apex with a mucronate tip which is not commonly preserved; at middle of shoot length ranges from 6 to 15 mm., width from 1 to 2 mm.; approximate average dimensions at middle of shoot 11 mm. by 1.4 mm.; closely spaced on shoots, branching off at angles commonly approaching 90 degrees, and seldom as low as 45 degrees; obliquely attached on decurrent bases which are prominent and extended obliquely down shoot to next pair of needles; many needles may be missing from shoots; midvein well defined; a dark spot at base of leaf may result from absence there of chlorophyll (judging from similar areas on modern leaves). PISTILLATE CONES globose to ovoid, in some cases oblate or elongate probably as a result of compression; ranging in diameter from 1.1 to 2.2 cm. for closed cones, up to 3.4 for open cones, averaging about 1.5 cm.; deciduous on elongate, commonly curving, leafless shoots from 2.1 to 6 cm. long, 1 mm. in diameter or rarely up to 2 mm. in the case of specimens which may be crushed; cone shoots have in all cases been shed before preservation; a group of scaly leaves may be seen at the base of well preserved cone shoots; cone scales peltate, decussately

attached, elongated transversely, concave with a medium[1] depression from which lines radiate to margin, 10 to 22 in number, averaging 12-16 on smaller cones, 18-20 on larger. SEEDS elongate, with curving wings notched distally, up to 5 mm. long and 4 mm. broad over all. STAMINATE CONES borne on specialized shoots; only detached shoots have been found, up to 8.5 cm. long, but association of groups on similarly oriented shoots suggests their attachment on panicles like those of the living species; borne laterally in decussate pairs which tend to be rotated into a single plane; in some instances more than one cone may develop on each side; in axils of slender foliage leaves which are rarely persistent; young cones globular, up to 2 mm. in diameter, becoming ovoid at maturity, up to 5 mm. long, 3 mm. in diameter; scales obscure, decussately arranged."

EMENDED DIAGNOSIS:[2]

FOLIAGE SHOOTS bearing dimorphic leaves, acicular except near the shoot base where they are scale-like and usually aggregated in a bulbous cluster; shoots of two types, persistent and deciduous. PERSISTENT SHOOTS bearing needles up to 5 cm. long and 3.5 mm. broad; needles generally decussately attached and rotated into flat sprays, but may appear sub-opposite or spirally arranged, particularly near the apex. Branchlets and deciduous shoots develop in the axils of leaves, generally in opposite pairs; subtending leaves may or may not persist.[3] DECIDUOUS SHOOTS ranging up to 9 cm. in length, bearing 10-30 pairs of leaves, generally decussately formed but usually rotated into a distichous position, otherwise appearing sub-opposite or spiraled. Leaves generally more closely arranged than on persistent shoots. LEAVES linear, obovate, or ovate, rounded at the base, usually petiolate, bluntly rounded at the apex with a mucronate tip with ideal preservation, otherwise apex more or less acutely tapering without evidence of a mucra.

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[1] It is suggested by this author that "medium" is incorrectly used here for "median".

[2] Unfortunately Chaney makes no distinction between a diagnosis and a description. A shortened, formal, emended diagnosis is presented here with a more general description following.

[3] An excellent account of branch development may be found in Chandrasekharam, 1972, complete with illustrations.

Leaf length ranging to a maximum of 3 cm. and width varying from 0.5 to 3 mm.; branching from the shoot at angles between 90 degrees and 45 degrees, more commonly nearer the former; attached on decurrent bases which extend obliquely down the stem to the next leaf, exhibiting a degree of twisting; a dark spot appearing at the base of the leaf which may be comparable to that of the extant species. PISTILLATE CONES globose to ovoid, occasionally elongate; ranging in diameter from 1-2.5 cm. for closed cones, up to 3.5 cm. for open cones; deciduous on long stalks up to 15 cm. in length; cone scales peltate, decussately attached, often elongated transversely, concave with a median depression. SEEDS elongate, with curving wings notched distally, up to 5 mm. long and 4 mm. broad over all.[1] STAMINATE CONES borne on simple or compound branching axes,[2] the fertile portions most commonly found detached, in which state they may reach a maximum of 9 cm.; cones are borne in the axils of successively opposite pairs of leaves, globular to ovoid in shape and reaching a maximum of about 5-6 mm. in length and 3 mm. in diameter; scales, when distinguishable, decussately arranged.

Description and Discussion of Emendation - Based on a study of the morphological range of variance exhibited by the extant *Metasequoia glyptostroboides* and the fossil species *M. occidentalis* from various localities (Figs. 41, 43-46) it is deemed reasonable that the diagnosis of the latter be sufficiently broadened to allow for these variants and to include those members of Cretaceous floras (including *M. cuneata*) which fall within the generic limitations. Characters previously listed as distinguishing *M. cuneata* and

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[1] As no well preserved specimens of seeds attributable to *M. cuneata* are known, and as no additional seed material of *M. occidentalis* was examined, Chaney's diagnosis of the seeds is left unemended.

[2] Whereas Chaney surmised the disposition of seed cones on branching systems, it is now documented by material from the Genesee locality, an account of which appears in Chandrasekharem (1972).

other taxa listed in synonomy with the new diagnosis from *M. occidentalis* can be demonstrated as present in recent and extant material. These characters include obovate leaves (visible in *M. occidentalis*, Figs. 42, 44), paucity of leaves on short shoots (visible in *M. occidentalis*, Figs. 43, 44), and sub-opposite or nearly spiral leaf arrangement (visible in *M. glyptostroboides*, Figs. 45, 46, and *M. occidentalis*, Fig. 42, apex).

The material of *Metasequoia* from the Smoky Tower locality may be seen to differ from material of similar age (Genesee locality) and from the extant species in some gross morphological features. These include the relative length of leaves subtending deciduous shoot and general L/W ratios of leaves on deciduous shoots. Leaves subtending branches in the extant species and in the Genesee material are typically much longer than leaves on the axillary branch (Figs. 40, 48). This difference is much less noticeable in the Smoky Tower *Metasequoia* (Fig. 39). The leaf L/W ratios of *M. occidentalis* and *M. glyptostroboides* (Figs. 37, 38, 40) are also much higher than the Smoky Tower material (Fig. 39). These differences may be due to the relative immaturity of the Smoky Tower specimens [as illustrated by the very young leaves at the tips of most shoots (Figs. 39, 42)] or to a variation in the phenotype expressed in the Smoky Tower population. In either case, these variants (which fall intermediate between the old *M. occidentalis* and *M. cuneata*) fall within the range of the

FIGURES 37-40.

Fig. 37. Specimen S162 - *Metasequoia occidentalis* (Newberry) Chaney from Genesee, Alberta, showing the opposite arrangement of branches and leaves. X 1.5

Fig. 38. Specimen 3525 - paratype of *M. occidentalis* from the Dugout Gulch, John Day Basin, Oregon; deposited in the paleobotanical collection, University of California, Berkeley. X 1.5

Fig. 39. Specimen S1924B - *M. occidentalis* from the Smoky Tower locality, Alberta, showing the opposite arrangement of leaves and the obovate shape of some needles. X 1.3

Fig. 40. Specimen of extant *Metasequoia glyptostroboides* showing the opposite nature of the branchlets and leaves. X 1

37

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39

40

FIGURES 41-46.

Figs. 41-44. *Metasequoia occidentalis* (Newberry) Chaney

Fig. 41. Specimen #90 - from the John Day Basin, Oregon; a deciduous shoot showing basal scale leaves and opposite long leaves; deposited in the Paleobotanical Museum, University of Oregon, Eugene. X 2

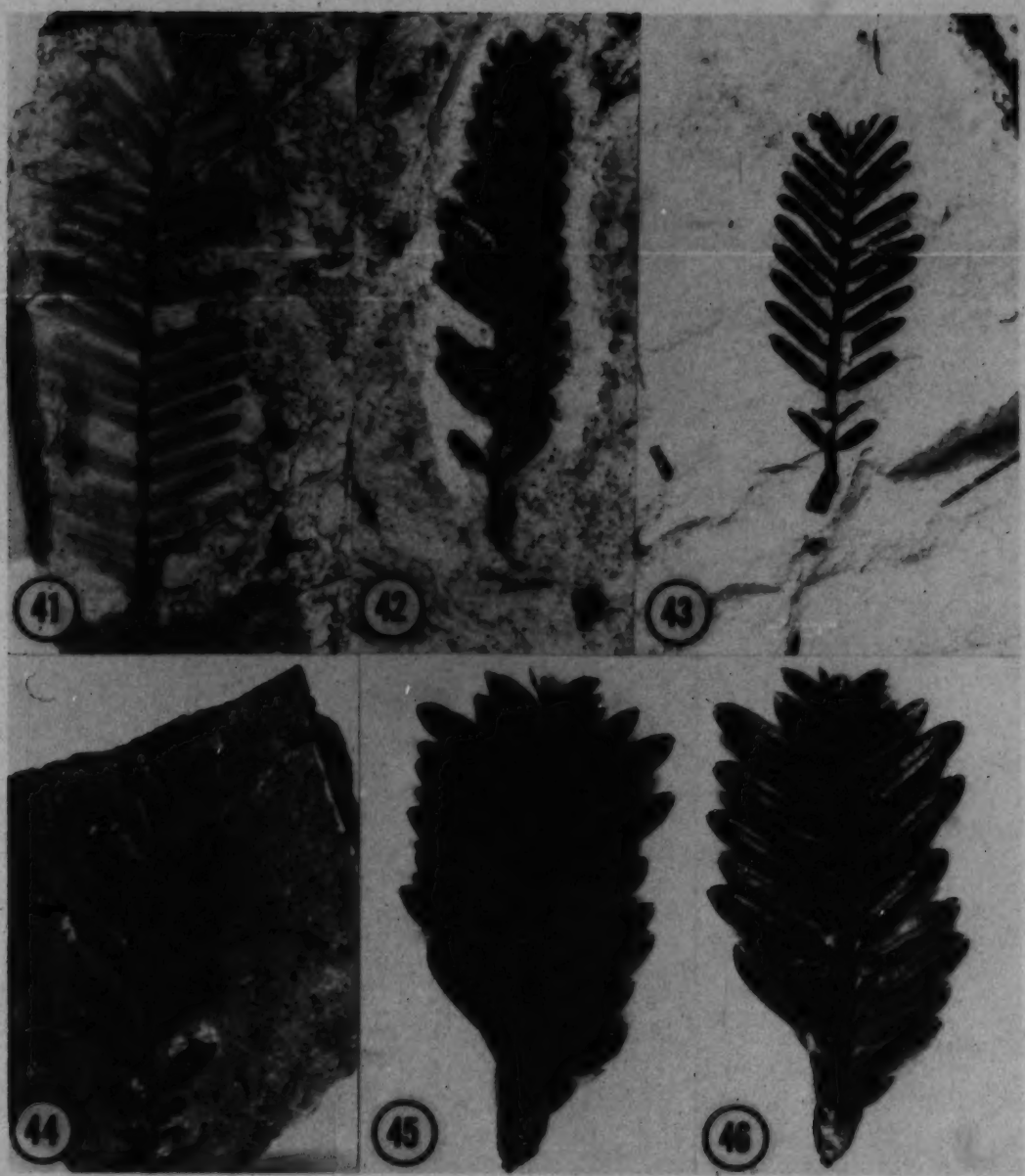
Fig. 42. Specimen S1949 - deciduous shoot from the Smoky Tower locality, Alberta, showing basal scale leaves and opposite pairs of long leaves. X 2

Fig. 43. Specimen S3402A - deciduous shoot from Genesee, Alberta, showing basal scale leaves and opposite long leaves. X 2

Fig. 44. Specimen 2463 - deciduous shoot from the Upper Cretaceous of Wyoming. Figured by Dorf (1942, Plate 6, Fig. 6) as *Sequoia dakotensis* Brown; opposite to subopposite leaves are visible; deposited in the paleobotanical collection, University of California, Berkeley. X 2

Fig. 45. Deciduous twig of extant *Metasequoia glyptostroboides* (abaxial surface) showing basal scale leaves and subopposite arrangement of long leaves. X 3

Fig. 46. Adaxial view of Fig. 45 showing the same features. X 3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FIGURES 47-49.

Fig. 47. Enlarged view of Fig. 40 (*Metasequoia glyptostroboides*) showing the very long leaves subtending the opposite branchlets. X 2.8

Fig. 48. Specimen S3151 - branching system of *Metasequoia occidentalis* from Genesee, Alberta, showing the very long leaves subtending the opposite branchlets. X 3

Fig. 49. *Metasequoia occidentalis* from the Smoky Tower locality, Alberta, showing the twisting, oblique nature of the petiole (B); unnumbered specimen is deposited in the private collection of Mr. B. Tiemons, Grande Prairie, Alberta. X 5.2

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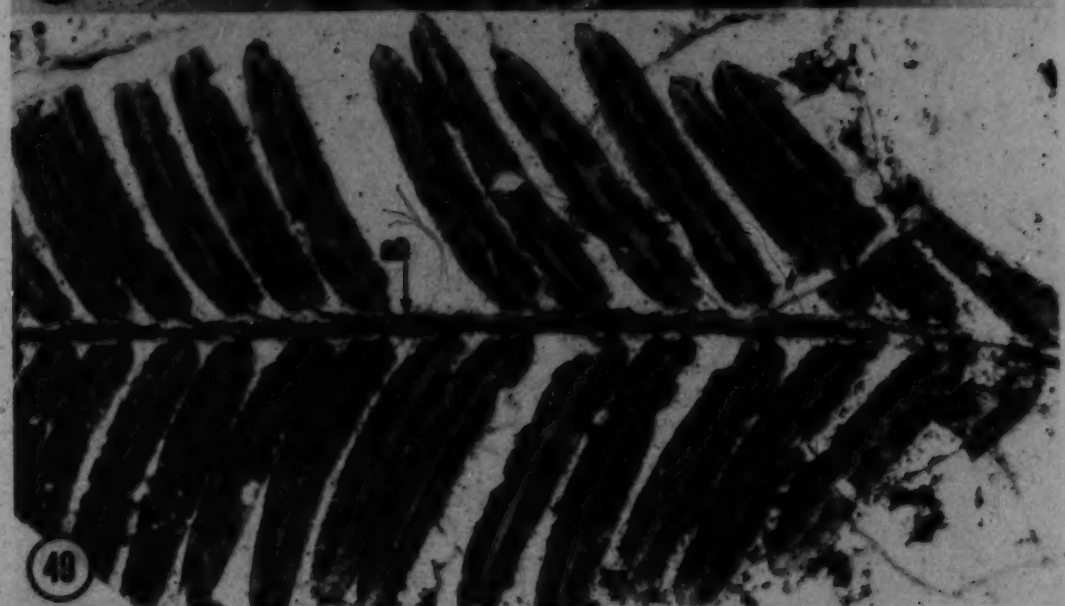

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emended diagnosis and are not considered great enough (in light of the variation exhibited by the single extant species) to warrant taxonomic recognition.

It might be argued from the preceding discussion of the genus that the fossil representatives now lumped into the single species *M. occidentalis* show sufficient variation among themselves and sufficient similarity to the extant species to be taxonomically combined with it. However, the arguments presented at the beginning of the systematic portion of this thesis for taxonomic separation of fossil and living species are applicable here and thus the synthesis of the two taxa is not supported.

Glyptostrobus nordenskioldii (Heer) Brown 1962

Glyptostrobus dakotensis Brown. 1936. Journ. Wash. Acad. Sci. 26(9): 355-356. Figs. 2-4 (including all synonomies listed).

Glyptostrobus oregonensis Brown. 1936. Journ. Wash. Acad. Sci. 26(9): 356-358. Fig. 1 (including all synonomies listed).

Glyptostrobus dakotensis Brown. Pabst. 1968. U. Cal. Publ. Geol. Sci. 76: 50-51. Plate 12, Figs. 1-3.

Juniperus washingtonensis Pabst. 1968. U. Cal. Publ. Geol. Sci. 76: 51. Plate 10, Figs. 7, 8. Plate 11, Figs. 1, 3, 4.

Glyptostrobus oregonensis Brown. Becker. 1969. Palaeontographica. Abt. B. Bd. 127. Plate 7, Figs. 21-27.

Description - By far the most abundant plant megafossils (excluding *Equisetum*) found at the Smoky Tower locality are

those now assigned to the genus *Glyptostrobus*. While the list of specimens studied indicates a total of 437 for this taxon, it would have been possible to raise that number to over 1000 if all specimens found at the locality had been numbered and added to the collection.

The Smoky Tower material contains specimens of all three foliar types listed by Brown (1936) - cupressoid, cryptomeroid, and taxodioid.[1] In addition to specimens showing various combinations of these leaf types, seed cones, cone scales, and possible pollen cones were collected.

The commonest foliage type is one exhibiting a leaf morphology which might be termed crypto-cupressoid, being intermediate in both size and shape (Figs. 50, 55, Text-Fig. 4). These are usually found as branching systems rather than individual deciduous branchlets (Fig. 50). Their leaves generally exhibit a spiral phyllotaxy, but sometimes they are preserved in a manner which gives the appearance of having a definite two-ranked arrangement (Fig. 55).

Other specimens that show a definite taxodioid leaf type were also found (Figs. 82, 85), as were many showing the transitional characteristics (Figs. 57, 59).

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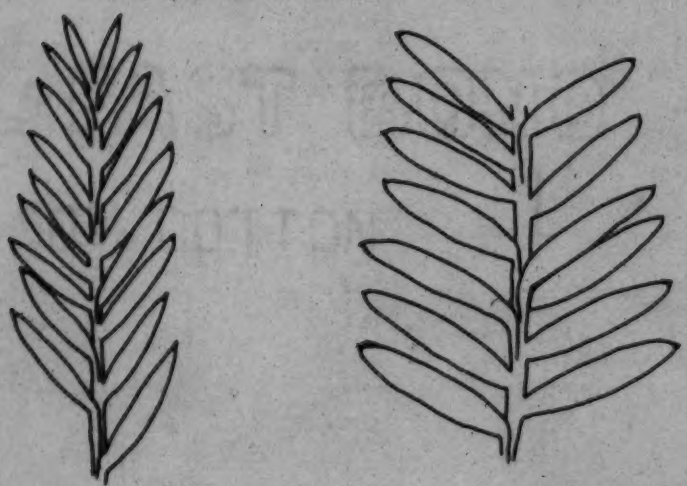
[1] Examination of the Smoky Tower locality material shows that much of the foliage, rather than fitting into one of these three standard categories, is intermediate. Therefore, the terms crypto-taxodioid and crypto-cupressoid will be used in this thesis to describe specimens of intermediate morphology. Examples of all five types are shown in Text-Fig. 4.



TEXT-FIGURE 4.

GLYPTOSTROBUS Leaf Types

The base of branchlets exhibiting taxodioid or crypto-taxodioid foliage often has scale leaves, arranged spirally. These spirals vary in tightness from extremely loose to very compact and appear bulbous (Figs. 57, 59).

Two hundred leaves of the crypto-cupressoid variety were measured, and it was found that the width measured at the widest point varied from 1.0 - 2.5 mm with the mean being 1.8 mm. The length varies from 3.0 - 7.0 mm with the average being 5.4 mm. The average L/W ratio proved to be 3.2:1. Of the 200 leaves examined, 158 proved to be widest at the middle, while 32 would be classed as obovate, with their greatest width near the apex. One hundred and forty-five of the 200 leaves show a tendency for the leaf tip to recurve toward the axis (Fig. 50, Letter R). This feature, however, could be the result of preservation, and of little diagnostic value.

One hundred leaves of the crypto-taxodioid variety were examined and similar observations made. The maximum width varies from 1.8 - 3.0 mm with the mean being 2.2 mm. The length varies from 8.0 - 19.0 mm with the mean being 13.4 mm. The mean L/W ratio was found to be 6.5:1. Seventy-eight leaves were observed to be relatively uniform in width (excluding the tapering apex), allowing them to be termed linear (or lanceolate), while 18 show a definite widening toward the base and are ovate. The 100 crypto-taxodioid leaves diverge from the axes at angles ranging from 90 degrees to 18 degrees, with the mean being 37

degrees. No pronounced degree of leaf-tip recurvation was observed in this leaf type. However, of the 82% of the leaves examined which show good preservation of the leaf tip, almost half show what could be interpreted as a mucronate tip (Fig. 65, letter M).

Difficulty was encountered in making quantitative observations on the scale leaves at the base of individual branchlets due in part to preservation and in part to their degree of compaction. It may be noted, however, that when found in a loose spiral they are similar in size and shape to the crypto-cupressoid variety discussed earlier. If there is any significance to be noted, it would be that the scale leaves nearest the base are shorter and display a lower L/W ratio. The additional observation may be made that on a given shoot (Figs. 57, 59) it is possible to observe a transition from scale leaves through crypto-cupressoid leaves to crypto-taxodioid leaves in a more acropetal position on the main axis. This observation, which helps to explain this author's use of combinations of Brown's leaf types, will be expanded upon in the following discussion.

While reproductive material was relatively scarce at the Smoky Tower locality, 8 specimens representing *Glyptostrobus* seed cones were recovered. These ranged from very immature (Fig. 76) to mature, fully opened cones (Fig. 72). All show thick, woody, imbricated cone scales with recurved, spine-like bract tips which typify the seed cones of the

genus. Where attachment is observed, it can be seen that the cones were borne terminally on branches bearing cupressoid or crypto-cupressoid leaves (Figs. 67, 72, 74). All cones collected were borne singly, with one exception where two cones were found on a single branching system (Fig. 73). Even in this case, however, each cone had a separate, leafy stalk.

Five specimens were collected showing detached seed cone scales which are tentatively assigned here to *Glyptostrobus*. These are roughly triangular in shape with an acute base and an apex showing 3-7 shallow, narrow lobes. In appearance they are similar to cone scales of the extant species, *G. pensilis* Koch. The size and shape of the fossil cone scales are comparable with scales still attached to mature cones (Fig. 71).

Six specimens were collected which showed numerous cupressoid leaf-bearing shoots with bulbous apices (Fig. 75) that may represent pollen cones. Dallimore and Jackson (1966) state that the pollen cones of *Glyptostrobus* are similar to those of *Taxodium*. The pollen cones of extant *Taxodium* do not, however, bear a strong resemblance to the fossil material described here, due to the compound nature of *Taxodium's* cone-bearing axes. However, examination of pollen cones from herbarium material of *Glyptostrobus pensilis* (Fig. 77) and also that figured by other workers for both *G. pensilis* and *G. oregonensis* Brown (Becker, 1969, Plate 7, Figs. 21-28) indicates that *Glyptostrobus* has pollen

cones more similar to *Sequoia* where cones are borne singly on the tips of axes having cupressoid leaves (Fig. 79). This being the case, the Smoky Tower material could well represent pollen cone fragments of *Glyptostrobus*, as may be seen by comparing Figs. 75 and 77. However, as no pollen was found in association with these fossil structures, it is possible that the material represents foliar buds of cryptocupressoid branches similar to those seen in Fig. 50, letter B.

Discussion - At the present time two distinct species are recognized for *Glyptostrobus* compression remains in North America. These are *G. nordenskioldii* (Heer) Brown and *G. oregonensis* Brown. The former extends from the Upper Cretaceous through the Eocene and the latter is a Miocene species. A European species, *G. europaeus* (Brongn.) Heer is widely recognized from Miocene deposits and is considered to differ significantly from the American counterparts (Brown, 1936, 1962). All of these are very similar to the extant species, *G. pensilis* Koch.

In no instance known to this author do the two North American species over-lap stratigraphically. Thus all three species are well separated either geographically or stratigraphically, and no immediate problems arise from keeping them as distinct nomenclatorial entities. However, a close examination of the two North American species, *G. nordenskioldii* and *G. oregonensis* shows that the similarities far outweigh the differences. Furthermore, the geologically older

species, *G. nordenskioldii*, bears at least as much similarity to the extant species, *G. pensilis*, if not more, than does *G. oregonensis*. Because of the morphological similarities between *G. nordenskioldii* and *G. oregonensis*, which will be discussed in detail in the following pages, it is proposed to combine the two species.

Although *G. oregonensis* was described in 1936, and *G. nordenskioldii* was described in 1963, *G. nordenskioldii* was a new combination based on *Sequoia nordenskioldii* Heer 1871 and thus this name has priority. *G. nordenskioldii* (Heer) Brown is, therefore, kept as the name for all North American Tertiary compression fossils previously described, and *G. oregonensis* Brown is placed in synonomy.

The Smoky Tower material assignable to *G. nordenskioldii* provides strong evidence for this combination of all North American glyptostroboid fossil material. Comparison of crypto-taxodioid foliage from the Smoky Tower locality (Fig. 52) with that from the type locality of *G. oregonensis* (Fig. 53) shows that there are striking similarities in leaf shape, size, and angle of attachment. Similar comparisons based upon crypto-cupressoid foliage from the same localities (Figs. 55, 56) lead to the same conclusion. None of the seed cones found at the Smoky Tower locality were at the same developmental stage as those studied from the Miocene of Oregon, and thus direct comparison was impossible. Indirect comparison or comparison of cones at different stages of development did yield some positive conclusions.

A cone from the extant species, *Glyptostrobus pensilis* (Fig. 71), was compared to one at a similar stage of development from the Smoky Tower locality (Fig. 72) and found to be extremely similar in scale size, shape, and mode of attachment. Also, a younger cone of *G. pensilis* (Fig. 69) was compared with the material of *G. oregonensis* (Figs. 66, 68, 70) and found to agree in basic characteristics. These similarities suggest that the seed cones of *G. nordenskioldii* and *G. oregonensis* are very similar.

Further comparison of the Smoky Tower material to that of the extant species, *G. pensilis* shows many other similarities. Shoots with cupressoid leaves were found in both groups to produce shoots bearing crypto-taxodioid foliage with no leaves of intermediate types (Figs. 50, 51). Likewise, the variability in the number and phyllotaxy of the scale leaves at the base of crypto-taxodioid deciduous shoots mentioned earlier for the Smoky Tower material was also found to be present in the extant *G. pensilis* (Figs. 62, 63). Similarly, the size, shape, and decurrent base of the crypto-taxodioid foliage was found comparable (Figs. 61, 64, 65). Even the mucronate needle tips on the shoots of Smoky Tower material were found present in roughly the same percentage in herbarium material. The above observations support the obvious conclusion that *G. pensilis* and the Smoky Tower *Glyptostrobus* are very closely related.

Material described from other localities as *Glyptostrobus nordenskioldii* is also comparable to the Smoky Tower

specimens. Chandrasekharam (1972) described eight specimens from the Genesee locality which he tentatively placed in the species. No reproductive structures were found associated with this material, however, and some hesitancy was expressed in identifying the specimens as *Glyptostrobus*. Comparison of one of the Genesee specimens (Fig. 54) with those of *Glyptostrobus* from other localities (Figs. 52, 53) shows a definite similarity in leaf size and shape, and in general shoot appearance. In addition, collectively the Genesee material exhibits all of the leaf types shown to be found in *Glyptostrobus* (Text-Fig. 4), leaving little doubt as to the validity of the identification by Chandrasekharam.

Material studied by Pabst (1968) from the Chuckanut Formation of northwestern Washington was also examined. Within this flora Pabst identified specimens belonging to the genera *Taxodium*, *Glyptostrobus* (*G. dakotensis* Brown), and *Juniperus*. Based on the specimens figured in the 1968 paper and those additional specimens housed in the paleobotanical collection, University of California, Berkeley, from the same collection, it is the opinion of this author that only specimens of the genus *Glyptostrobus* demonstrate suitable characteristics for confident identification. The material identified as *G. dakotensis* by Pabst compares favorably to the Smoky Tower material, and is thus considered a synonym of *G. nordenskioldii*. The most prevalent foliar types are cupressoid and crypto-cupressoid (Figs. 60, 60a). The presence of a cone scale (Fig. 60) is the main

basis for Pabst's identification (Pabst, 1968, p. 50). Interestingly enough, a far more convincing specimen in the Berkeley collection originated from the same locality (Fig. 78). It shows several attached cones with definite glyptostroboid affinities, and makes a much stronger case for the identification.[1]

In the same paper Pabst describes a new species of conifer, *Juniperus washingtonensis*. The description is based on both foliage and seeds supposedly assignable to *Juniperus*. However, the specimen figured as the holotype (Pabst, 1968, Plate 11, Fig. 4) and other figured specimens belonging to this taxon (Pabst, 1968, Plate 11, Figs. 1, 3), and which supposedly show seeds, illustrate no positive attachment between the vegetative and reproductive parts. More important, the foliage in these specimens is identical with that identified as *Glyptostrobus dakotensis* and shown with an accompanying glyptostroboid cone scale (Fig. 60). In addition, Pabst states in the text (p. 50) that "the plant [*Glyptostrobus*] is deciduous, with slender twigs

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[1] Pabst's 1968 paper was published posthumously and represents work done by her for her doctoral dissertation prior to her death in 1963. The paper was compiled by Drs. R.W. Chaney and W.L. Fry and Mr. H. Schorn of the University of California, Berkeley. In personal communications with the latter two workers it was found that some of the original specimens described in the thesis could not be located at the time that the paper was published, and thus some of the original author's statements had to be accepted without documentation. Any observations and conclusions in this thesis that are at variance with Pabst's 1968 paper are probably the result of difficulties encountered by the compilators in interpreting and documenting the original work.

bearing two types of leaves; one short and oppressed, similar to *Juniperus* foliage....." This statement is taken as an acknowledgement of the similarity of the two genera. Because of the difficulties stated in the footnote on the preceding page, it is impossible to say that *Juniperus* was not a member of the Chuckanut flora. However, the specimens observed by this author and figured by Pabst (1968) do not justify placement in that genus and are herein synonomized with *Glyptostrobus nordenskioldii*.

Pabst also notes the presence of *Taxodium* in the Chuckanut flora. In the text she mentions numerous cones and twigs of this genus as being the dominant members of the flora at one of the localities. The figured specimens show only three deciduous shoots bearing taxodioid foliage (Fig. 60a, taken from Pabst, 1968, Plate 9, Fig. 3). In the text (p. 49), Pabst cites Chaney's (1951) Figs. 1-2 of Plates 9, 10 as evidence for *Taxodium* in the Chuckanut Formation. Here again, however, the figures referred to show only vegetative shoots with taxodioid foliage. On this minimal evidence it seems unwise to accept *Taxodium* as a valid member of this flora, particularly since another genus possessing taxodioid foliage, *Glyptostrobus*, has been well documented as being present.

Conclusions - Perhaps the most abundant remains at the Smoky Tower locality have proven to be *Glyptostrobus nordenskioldii* (Heer) Brown. Identification is based on the presence of all major forms of glyptostroboid leaves, seed cones at

various stages of maturity, cone scales, and the presence of possible pollen cones.

A comparison of the Smoky Tower material with other specimens of *G. nordenskioldii*, the Miocene species, *G. oregonensis*, and herbarium and fresh material of the extant species *G. pensilis* shows very close similarities among all of them. These characteristics have led this author to the conclusion that all the fossil material should be included within one species. On the basis of priority, the valid species is then *G. nordenskioldii*, and *G. oregonensis* is placed in synonomy.

The author's study of other material already cited with similar morphological characteristics from the Chuckanut Formation of Washington (Figs. 60, 60a, 78) has led to the conclusion that much of this material placed by Pabst in the species *Glyptostrobus dakotensis* and *Juniperus washingtonensis*, should also be placed in synonomy with *Glyptostrobus nordenskioldii*.

Relations within the Taxodiaceae - In 1951 Professor Chaney published an excellent historical account of some genera of the Taxodiaceae in North America. In addition to the historical review, he made sweeping taxonomic changes to incorporate the recently discovered genus *Metasequoia* into the literature. But most important he devised a system for separating the fossil *Taxodium*, *Sequoia* and *Metasequoia* of North America. Unfortunately this latter system, which has proven excellent for many specimens and many floras, has

FIGURES 50-56.

Fig. 50. Specimen P67.1.83B - *Glyptostrobus nordenskioldii* from the tuff horizon showing the production of a shoot bearing crypto-taxodioid foliage from a bud (letter B) of a branch bearing crypto-cupressoid foliage; letter R indicates a recurved leaf apex typical of the Smoky Tower material; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 2.6

Fig. 51. Specimen of extant *Glyptostrobus pensilis* showing the same features shown by *G. nordenskioldii* in Fig. 50; letter B indicates a bud. X 2.5

Fig. 52-56. *Glyptostrobus nordenskioldii* (Heer) Brown

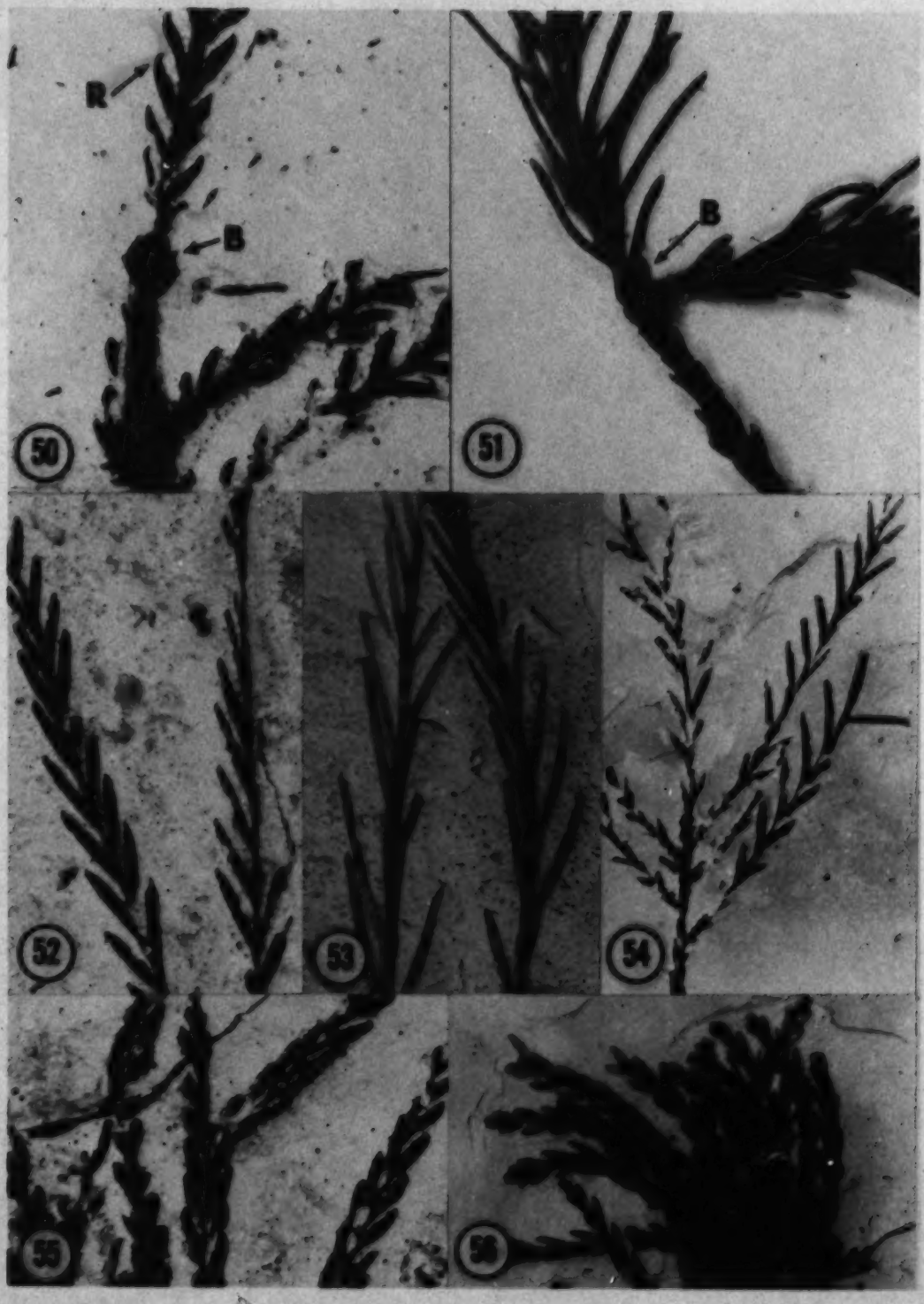
Fig. 52. Specimen S2876B - crypto-taxodioid foliage from the tuff horizon; many leaves also display mucronate tips. X 1.6

Fig. 53. Specimen 2885 - crypto-taxodioid foliage (formerly *G. oregonensis*) from the Miocene of Oregon; deposited in the paleobotanical collection, University of California, Berkeley. X 1.6

Fig. 54. Specimen S3152 - a shoot from the Genesee locality showing crypto-taxodioid foliage. X 1.3

Fig. 55. Specimen P66.8.37A - crypto-cupressoid foliage from the tuff horizon preserved in such a manner as to give the appearance of opposite leaves; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 2.5

Fig. 56. Specimen 2885 - crypto-cupressoid foliage (formerly *G. oregonensis*) from the Miocene of Oregon; deposited in the paleobotanical collection, University of California, Berkeley. X 2.1


R
B
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B
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FIGURES 57-60a.

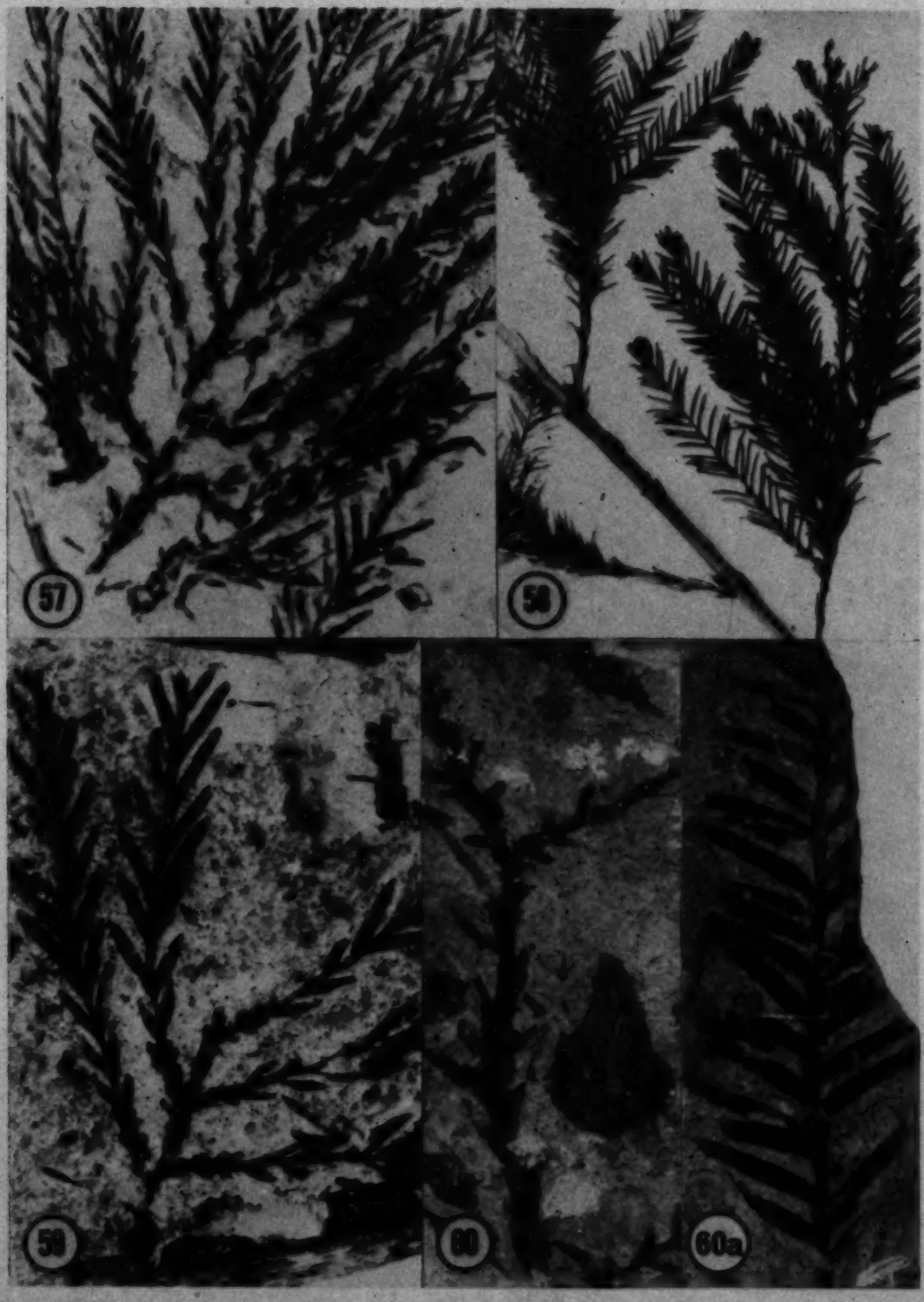
Fig. 57. Specimen S2771 - a shoot of *Glyptostrobus nordenskioldii* with numerous branchlets showing a progression from cupressoid leaves at the base of each branchlet through crypto-taxodioid foliage near their apices. X 1.2

Fig. 58. Specimen of extant *Glyptostrobus pensilis* showing branches bearing primarily taxodioid leaves; from herbarium sheet #232838, University of California, Berkeley. X .8

Fig. 59. Specimen S2932A - shoot of *Glyptostrobus nordenskioldii* from the tuff horizon showing the progression from cupressoid basal foliage to apical crypto-taxodioid foliage on each branchlet. X 1.6

Fig. 60. Specimen 10543 - *Glyptostrobus nordenskioldii* from the Chuckanut Formation, Washington, showing a twig and a seed cone scale; deposited in the paleobotanical collection, University of California, Berkeley. X 4

Fig. 60a. Specimen 10541 - a taxodioid branchlet from the Chuckanut Formation, Washington; deposited in the paleobotanical collection, University of California, Berkeley. X 3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58
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60a

FIGURES 61-65.

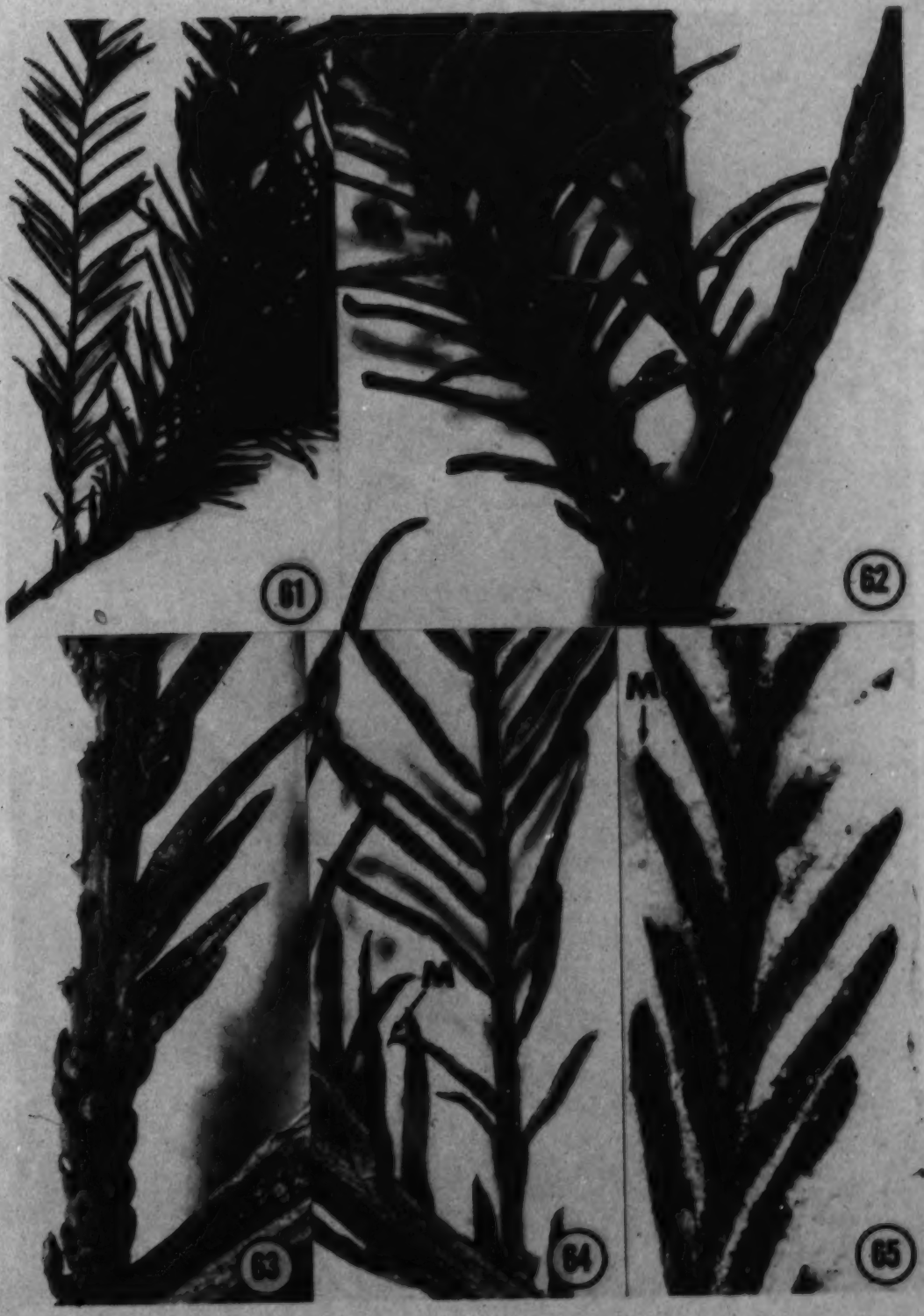
Fig. 61. Specimen of extant *Glyptostrobus pensilis* showing branches with crypto-taxodioid leaves and without basal cupressoid leaves; from herbarium sheet #232838 deposited at the University of California, Berkeley. X 1.4

Fig. 62. Specimen of extant *G. pensilis* showing the variation in compaction of cupressoid (scale) leaves at the base of branches; from herbarium sheet #258434 deposited at the University of California, Berkeley. X 3

Fig. 63. Enlarged view of the base of a branch of *Glyptostrobus pensilis* showing several tiers of cupressoid leaves; from herbarium sheet #258434 deposited at the University of California, Berkeley. X 9

Fig. 64. Enlarged view of Fig. 62 showing closely packed basal cupressoid leaves and the pronounced mucronate tip (letter M) typical of many crypto-taxodioid leaves. X 3

Fig. 65. Specimen S1857 - crypto-taxodioid foliage of *G. nordenskioldii* showing the typical mucronate leaf tip (letter T). X 5


B1
B2
M
M
B3
B4
B5

FIGURES 66-70.

Figs. 66-70. *Glyptostrobus* seed cones.

Fig. 66. Specimen 2881 - *G. nordenskioldii* (formerly *G. oregonensis*) from the Miocene of Oregon; shows mature seed cones on branches possessing cryptocupressoid foliage; deposited in the paleobotanical collection, University of California, Berkeley. X 1.25

Fig. 67. Specimen P67.1.114 - fairly mature seed cone of *G. nordenskioldii* from the tuff horizon, Smoky Tower locality, showing cupressoid and cryptocupressoid foliage on adjacent branches; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 1.3

Fig. 68. Specimen 2886 - *G. nordenskioldii* (formerly *G. oregonensis*) from the Miocene of Oregon; deposited in the paleobotanical collection, University of California, Berkeley. X 1.5

Fig. 69. Seed cone of extant *G. pensilis* showing cupressoid and cryptomeroid foliage on adjacent branches; from herbarium sheet #363140 deposited at the University of California, Berkeley. X 1.5

Fig. 70. Specimen 2887 - *G. nordenskioldii* (formerly *G. oregonensis*) from the Miocene of Oregon, showing the typical imbricate cone scales and spinose bract tips; deposited in the paleobotanical collection, University of California, Berkeley. X 1.9

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X
3885

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FIGURES 71-74.

Fig. 71. Seed cone of extant *Glyptostrobus pensilis* from herbarium sheet #363140, University of California, Berkeley; shows the thick, imbricate cone scales of a mature cone and the cupressoid leaves of the cone stalk. X 3

Fig. 72. Specimen S2773 - mature seed cone of *Glyptostrobus nordenskioldii* (Heer) Brown from the Smoky Tower locality showing the thick, imbricate cone scales and the cupressoid leaves of the cone stalk. X 3

Fig. 73. Specimen P66.8.55 - two mature seed cones of *G. nordenskioldii* borne on individual scaly stalks, but part of the same branching system; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 3.8

Fig. 74. Specimen P67.1.114 - enlarged view of Fig. 67 showing attachment of the seed cone to a branching system bearing crypto-cupressoid leaves; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 3.1

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FIGURES 75-79.

Fig. 75. Specimen P66.8.33C - *Glyptostrobus* shoots from the tuff horizon showing bulbous apices which may be pollen cones; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 2.2

Fig. 76. Specimen S1620 - a twig of *Glyptostrobus* from the tuff horizon showing a probable young seed cone. X 2.2

Fig. 77. Twigs of extant *Glyptostrobus pensilis* showing pollen cones at the ends of branches having cupressoid leaves; from herbarium sheet #243828, University of California, Berkeley. X 2.3

Fig. 78. Specimen of *Glyptostrobus nordenskioldii* from the Chuckanut Formation, Washington, showing attached seed cones; unnumbered specimen deposited in the paleobotanical collection, University of California, Berkeley. X 3

Fig. 79. Specimen 3547 - *Sequoia affinis* Lesquereux from Florissant, Colorado, showing pollen cones; deposited in the paleobotanical collection, University of California, Berkeley. X 2

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associated with it certain assumptions and omissions which render its usefulness questionable when dealing with many fossils.

Perhaps the most obvious omission of the identification system devised in Chaney's 1951 paper is the exclusion of the genus, *Glyptostrobus*. It is to Chaney's credit that he recognized the genus as being present in the floras under consideration, as is obvious from the following statement (Chaney, 1951, p. 177):

> "The genus *Glyptostrobus* will be omitted from this discussion, largely because the material representing this genus may be more readily recognized, and has not been so generally confused. Brown has pointed out the distinguishing characters of *Glyptostrobus*, and has made a satisfactory revision of the American fossil species assigned to this genus (1936)."

Unfortunately, Brown (1936) does not make as clear a case for the uniqueness of *Glyptostrobus* as might be gathered from Chaney's remark. On pages 354-355 Brown states:

> "Although the living species, *Glyptostrobus pensilis*, can now be distinguished readily from species of *Taxodium* and other coniferous genera, the detection and separation of the fossil representatives of *Glyptostrobus* is fraught with considerable uncertainty. This is particularly true when foliage only is available. In the living species this may be of three kinds - cupressoid, taxodioid, and cryptomeroid, in allusion to the typical foliage, respectively, of *Cupressus*, *Taxodium*, and *Cryptomeria*. A given fossil shoot or twig with this range might therefore merit any one of four interpretations, let alone being confused with other genera, such as *Sequoia*, *Cunninghamia*, *Torreya*, *Juniperus*, *Tsuga*, etc. Because of the uncertainty concerning the identity of such twigs as are ordinarily preserved in shale and sandstone, those recorded fossil species of *Glyptostrobus* based upon foliage alone will not be discussed here but will be regarded as doubtful identifications."

Chaney has summarized the distinguishing characters for the three genera in tabular form on page 180 of his 1951 paper. Three of the five characters listed for their separation are foliar. Based on the above quotation from Brown (1936) these three characteristics are not valid unless *Glyptostrobus* also is considered. For the purpose of comparison, Chaney's table, with an additional column for *Glyptostrobus* has been reproduced for this thesis (Text-Fig. 5). In the following paragraphs each of the five characters will be reexamined in the light of the Smoky Tower material and further studies made by this author and others subsequent to Chaney's work.

1. Long shoots - it may be seen that even with the inclusion of *Glyptostrobus*, the only genus showing any difference in this category is *Metasequoia*. However, based upon examination of shoots from the extant species, *M. glyptostroboides*, some specimens of *M. occidentalis* (discussed earlier in this chapter), and material shown by Beck (1969, Fig. 18), it may be noted that occasionally *Metasequoia* also displays some degree of spiral phyllotaxy and alternate shoot production near the apex of an axis. It should also be mentioned here that Chaney specifically entitled his table "Distinguishing Characters of *Fossil* Specimens". However, if we are to accept these fossils as members of extant genera (which indeed has been done for all genera included in the table excepting *Metasequoia*), then we must assume that the initial assignment to this genus was based on

comparison with the extant species. Therefore, characteristics of the extant species relevant to the categories of the table must also be considered here, as they represent forms which we might expect to occur in the fossil record. Objection to the terms "long shoot" and "short shoot" have already been raised earlier in the chapter based upon living material. They are used here in conjunction with the fossils only to allow Chaney's table to be reproduced and studied in the terms he used.

2. Short shoots - Under this category Chaney lists five characteristics. The first of these, stem thickness, is a relative measure, and, because of variable thicknesses observed in *Glyptostrobus* axes, it is of questionable value. The second characteristic, phyllotaxy, has as questionable a value as it did for the long shoots, since *Metasequoia* will on occasion appear sub-opposite or spiral (particularly near the apex), and *Taxodium* will often appear sub-opposite, and not spiraled (Figs. 80, 83). The third characteristic, leaf disposition, is really directly connected to the second characteristic, and subject to the same variability. The fourth characteristic, leaf type and shape, is one which is unfortunately not nearly as clear-cut as the table would have the reader believe. To begin with, *Metasequoia* is not monomorphic, but dimorphic, having definite clusters of scale leaves at the base of deciduous shoots. Scale leaves were not really considered in any of the columns on Chaney's table. Therefore, to be accurate,

the number of leaf types for each genus in Chaney's chart must be increased by one. *Glyptostrobus*, as has been discussed and as is shown in Text-Fig. 4, has leaves which may be termed polymorphic. Strictly speaking, *Metasequoia* is the only genus which is strictly dimorphic and not polymorphic in that the other genera all produce leaves of intermediate types.

The final characteristic, persistence of the shoot, is not a good taxonomic character because it is, to a large degree, a function of the environment. In addition, *Sequoia*, listed by Chaney as having persistent shoots, (1951, p. 178), "In the case of the living *S. sempervirens*, ...short shoots may remain on the tree for three or four years;" does occasionally become deciduous. Chaney's uncertainty is amplified by the opening phrase of the same paragraph just quoted - "The deciduous foliar units of all three genera....." Thus this character is not one readily usable.

3. Leaves - For this category Chaney lists seven criteria. The first is not a "distinguishing character", as the original table title would suggest, in that all genera are described in the same term, acicular. The second characteristic, presence or absence of a petiole, is basically correct as described by Chaney, with the added *Glyptostrobus* not usually narrowing at the base and not possessing a petiole. As is shown by the specimens in Figs. 52, 64, however, this character is definitely variable, and

definitely dependent on preservation. Thus the character is good only after averaging large numbers of specimens.

The third characteristic, possession of a mucronate tip, may be treated in the same fashion as the first characteristic. That is to say, as Arnold and Lowthar (1955) have pointed out that *Taxodium* may possess a mucronate tip, and as *Glyptostrobus* may also (Fig. 64M), the character is uniform in all genera and not useful for differentiation.

The fourth character, angle of leaf divergence, has been thoroughly discussed for both *Metasequoia* and *Glyptostrobus* earlier in the text. In this discussion it is shown that in both instances the angle is much more variable than the chart would indicate. Characters five and six, midrib appearance and basal dark spot, respectively, are highly dependent on preservation. The former is too subjective to be useful, and the latter is valuable only as an infrequently occurring supporting character. When a dark spot is present, it adds weight to placement of the specimen in *Metasequoia*, but its absence (as is the common condition in all four genera) has no meaning as far as identification is concerned.

The final characteristic, mode of leaf attachment, is considered by Chaney, and by some later workers (Chandrasekharam, 1972) to be very important. Examination of numerous fossil and extant specimens has led this author to the conclusion that the character's main importance is that it

aids in elimination of one or two genera but it is not a character that allows positive identification. For example, it can be stated that a leaf obliquely attached to the stem and to some degree obliquely trending down the stem will not be the leaf of *Taxodium* or *Glyptostrobus*. By the same token, a leaf squarely joined and trending parallel to the stem will not be the leaf of *Metasequoia*. One might expect that a squarely joined, parallel base would also make placement in *Sequoia* unlikely. However, observation of herbarium material has shown that even the slight compression received in a plant press oftentimes "untwists" the leaf base, leaving it similar in appearance to *Taxodium* and *Glyptostrobus*. As this is the case in slightly pressed specimens, it is impossible to judge the potential effect of the compression undergone in the formation of most fossils. As is stated earlier in the chapter in a quotation from Brown (1936), it is virtually impossible to distinguish the foliage of *Taxodium* and the taxodioid foliage of *Glyptostrobus*. This author has looked at over 1000 specimens of these two genera, and his observations support those of Brown.

4. "Pistillate" (seed) cones - The characteristics listed for this category are basically correct, and may be used accordingly. However, several areas of caution must be observed. *Glyptostrobus* cones differ from all others in that they have non-peltate, imbricate cone scales. However, a *Glyptostrobus* cone by itself, or on its scaled stalk, may

be easily confused with a cone of *Cryptomeria*, which is almost identical. Similarly, when attached, cones of *Metasequoia* may be easily identified by their long, naked stalks. When detached from their stalks, however, the only major characteristic separating them from those of *Sequoia* is the decussate rather than spiral arrangement of cone scales. This can be a very difficult feature to assess, particularly in light of the genus *Parataxodium* Arnold and Lowthar (1955), which exhibits a cone scale attachment that is morphologically intermediate. In addition, in spite of the fact that Chaney stated that no attachment for *Taxodium* cones has been noted in the fossil record, the footnote to his table, mentioning that the extant species have cones borne on stalks similar to *Sequoia*, should alert the experienced observer that a single cone attached to a short stalk collected at a new locality could well be *Taxodium*, and not necessarily *Sequoia*. The persistence of the scales, as with the short shoots, is not a good taxonomic character.

5. "Staminate" (pollen) cones - The chief value of this category, as was the case with mode of leaf attachment, is to separate the four genera into groups. *Sequoia* and *Glyptostrobus* may be separated readily from the other two genera but are practically indistinguishable from each other (Figs. 77, 79). In the same way, *Metasequoia* and *Taxodium* are similar, separable only by the decussate or

TEXT-FIGURE 5. Comparative features of *Metasequoia*, *Sequoia*, *Taxodium*, and *Glyptostrobus*.

	METASEQUOIA	SEQUOIA	TAXODIUM	GLYPTOSTROBUS
Long shoots	Bearing shoots in opposite pairs, forming flat sprays	Bearing alternate shoots, forming flat sprays, or retaining spiral position on terminal axis	Bearing alternate shoots, forming flat sprays, or retaining spiral position on terminal axis	Bearing alternate shoots, forming flat sprays, or retaining spiral position on terminal axis
Short shoots	Stem slender Phyllotaxy decussate Leaves disposed distichously except on growing tips Monomorphic, acicular Deciduous	Stem stout Phyllotaxy spiral Leaves disposed distichously except on terminal branches where position persists Dimorphic, acicular except on terminal branches, there scaly Persistent	Stem slender Phyllotaxy spiral Leaves disposed distichously except on terminal branches where spiral position persists Dimorphic, acicular except on terminal branches, there scaly Deciduous	Stem slender - stout Phyllotaxy spiral to sub-opposite Leaves disposed distichously except on terminal branches where spiral position persists Trimorphic, being cryptomeroid, taxodioid, or cupressoid Usually deciduous
Leaves	Mostly acicular Narrowed at base, petiolate Apex obtuse, mucronate Angle of divergence high Midrib conspicuous Dark spot at base Decurrent base prominent, obliquely joined, obliquely trending along stem	Mostly acicular Not narrowed at base, sessile Apex obtuse, mucronate Angle of divergence intermediate Midrib less conspicuous Decurrent base prominent, obliquely joined, less obliquely trending along stem	Mostly acicular Narrowed at base, petiolate Apex acute Angle of divergence low Midrib conspicuous Decurrent base not prominent, squarely joined, trending parallel with stem axis	Mostly acicular Generally not narrowed at base, non-petiolate Apex acute to obtuse, often mucronate Angle of divergence intermediate Midrib conspicuous Decurrent base not prominent, squarely joined, trending parallel with stem axis
Pistillate cones	Deciduous Scales decussate Scales persistent Attached on long, naked stalk with basal scales	Commonly persistent Scales spiral Scales persistent Attached on short, scaly stalk	Deciduous Scales spiral Scales commonly deciduous No attachment noted	Usually persistent for at least one season Scales spiral Scales commonly deciduous Attached on short, scaly stalk
Staminate cones	Borne on specialized shoots Decussate, commonly in pairs Bracts decussate	Solitary on terminal or short lateral branchlets Bracts spiral	Borne on specialized shoots Spiral, alternately attached Bracts spiral	Solitary on terminal or lateral, unspecialized branchlets Bracts spiral

spiral nature of specialized shoots. Even their separation is made less significant by the presence of *Parataxodium* in the fossil record.

Having thus questioned the validity of many of the distinguishing characters used by Chaney and questioned the stability of others, it is necessary to consider the positive aspects of distinguishing between the four genera listed in the table (Text-Fig. 5). There are two important premises which must be mentioned before any specific details are considered. These are (1) that positive identification can be made only where a statistically significant number of specimens is available except where exceptional preservation is encountered, and (2) that identifications must be based on agreement of an aggregate of characteristics, and not on one single characteristic. An additional consideration which cannot be emphasized too often is that we are dealing with a group of plants which span 60 million years of time. In a family such as the Taxodeaceae, whose extant genera and species overlap in many characteristics, it must be expected that during these 60 million years, evolution has produced many different combinations of these overlapping characteristics. Therefore, there is no one criterion or set of criteria that can be applied for identification of a given fossil or a group of fossils.

In the following paragraphs a genus by genus summary is presented, listing the more constant characteristics which may be used in identification. It is in no way a key that

can be applied for the separation of the genera *per se* and is better interpreted as a set of guidelines to be used in association with comparative herbarium material and other, satisfactorily identified fossil specimens.

1. *Metasequoia* - Branches are usually borne in opposite pairs, subtended by a pair of opposite leaves. The leaves are regularly dimorphic, consisting of acicular, mucronate leaves along most of the axis and clusters of scale leaves at the base of deciduous shoots. The leaves are usually borne in a decussate arrangement, often appearing sub-opposite. The leaf bases are attached obliquely and trend obliquely down the stem. Seed cones are borne on long naked stalks with peltate cone scales. Pollen cones are borne on specialized shoots.

2. *Sequoia* - Branches are borne alternately. The leaves are mucronate, ranging from flattened acicular (as in *Metasequoia*) to scale-like, with various intermediate forms being common. The leaves are borne spirally, with a subopposite appearance common. The leaf bases are attached obliquely in most cases, with a tendency to trend obliquely down the stem. Preservation may give the impression of squarely joined bases trending down the stem in a near parallel fashion. Seed cones are borne on scaly axes with peltate cone scales. Pollen cones are borne terminally on unspecialized axes.

3. *Taxodium* - Branches are borne alternately. The leaves are mucronate, ranging from flattened acicular to scale-like as in *Sequoia*. They are borne spirally but often appear sub-opposite. Leaf bases are attached squarely and trend down the stem parallel to the axis. Seed cones usually are unattached, but when attached they are similar to *Sequoia*. Pollen cones are borne on specialized axes.

4. *Glyptostrobus* - Branches are borne alternately with a possible sub-opposite appearance. The leaves are mucronate, polymorphic, with crypto-taxodioid and crypto-cupressoid types most commonly occurring (Text-Fig. 5). Leaf bases are attached squarely, trending downward parallel to the axis of the stem. Seed cones are borne terminally on short, scaly stalks. Cone scales are non-peltate, imbricate, with spinose projections from the scale bracts. Pollen cones are borne on unspecialized shoots as in *Sequoia*.

The above criteria, when used in conjunction with comparative fossil and extant material, are useful only on large, moderately or better preserved suites of fossils. Unfortunately, a genus of taxodiaceous plants will often be represented by only a few specimens in a given flora. It is the opinion of this author, as substantiated by the preceding pages, that such material <u>cannot</u> be accurately identified at the generic level except in extremely rare cases of ideal preservation. This situation should cause no problems if its ramifications are realized by all workers

in the field, and such material consequently identified as *Incertae sedis*. Unfortunately this is not the case, as is witnessed by the many tentative identifications based on fragmentary specimens found in the literature.

To attempt to eliminate such possible misidentifications and the misinterpretations based on them, it is proposed in this thesis to create a new form genus for taxodiaceous foliar remains which cannot be positively assigned to specific genera. The artificiality of the genus is understood by its author, and justified by the rationalization that such a genus is a better repository for material where identification is uncertain than a previously well-established genus, placement in which might lead to erroneous paleoecological and phytogeographic conclusions.

Taxodiophyllum gen. nov.

Generic Diagnosis - Foliar shoots bearing leaves in either spiral or sub-opposite manner. Leaves taxodioid, crypto-taxodioid, cryptomeroid, crypto-cupressoid, or cupressoid, with or without mucra present. Leaf base attached either squarely or obliquely and trending down the stem either slightly obliquely or parallel to the shoot axis. Leaves acicular, lanceolate, ovate, linear or obovate.

Type species - *Taxodiophyllum cordillarum* Christophel sp. nov.

Taxodiophyllum cordillarum sp. nov.

Taxodium dubium (Sternberg) Heer. Chandrasekharam, 1972. Unpubl. thesis. Plate 39, fig. 244; Plate 7, Fig. 39,40.

Taxodium dubium (Sternberg) Heer. Mathews and Brooke, 1971. Syesis. Vol. 4, Figs. 5,6.

Sequoia affinis Lesquereux. Mathews and Brooke. 1971. Syesis. Vol. 4, Figs. 7-9.

Species diagnosis - Foliar shoots bearing from 12-50 leaves arranged in either a spiral or sub-opposite manner. Leaves taxodioid, crypto-taxodioid, cryptomeroid, crypto-cupressoid, or cupressoid, ranging in maximum width of the leaf from 0.1 mm - 4 mm and in length from 1.0 - 40.0 mm; with or without mucra. Leaf base attached either obliquely or squarely and trending in an oblique to parallel fashion down the axis. Leaves acicular, lanceolate, ovate, obovate, linear or spatulate.

Holotype - Specimen S1040 (Figs. 81, 84) which is deposited in the paleobotanical collection, Department of Botany, University of Alberta, Edmonton.

Locality - Genesee, Alberta (Chandrasekharam, 1972)

Discussion - The specimen listed as the holotype of the species was described as *Taxodium dubium* by Chandrasekharam in 1972. At this time he stated that due to the small number of specimens collected, the identification was somewhat questionable. The main criterion used by that author to distinguish the specimens from *Glyptostrobus* was the

bulbous disposition of scale leaves found on some of the deciduous shoots. However, a study of fossil and extant *Glyptostrobus* made earlier and presented in this thesis has shown that the range of disposition of scale leaves in *Glyptostrobus* includes a form displaying a tight spiral (somewhat bulbous) at the base. Therefore, as only eight specimens were collected, it seems that placing the material in the genus *Taxodiophyllum* is much safer.

Similarly, the material from Quilchena, British Columbia (Mathews and Brooke, 1971), is placed in the genus due to the fragmentary nature of the material and the paucity of specimens. It is beyond the scope of this thesis to make a thorough search of the literature for possible additional synonomies. It is hoped, however, that future workers will use the new genus for specimens where identification is questionable. The diagnosis has been made particularly flexible to accomodate and encourage its use on a diversity of specimens.

Summary - Within the family, Taxodiaceae, four genera, *Metasequoia*, *Sequoia*, *Taxodium*, and *Glyptostrobus* show a high degree of similarity in both extant and extinct species. In 1951 Chaney presented a thorough review of the first three of these genera and suggested a list of criteria for distinguishing between their fossil species.

Based upon a thorough study of the members of the Taxodiaceae present at the Smoky Tower locality and upon further studies of extant material and fossil material from

other localities, this author has undertaken a reexamination of Chaney's criteria with the inclusion of the genus *Glyptostrobus*. This reexamination has shown that the distinguishing characters are not nearly as constant as indicated by Chaney in 1951, and that a large amount of overlap, particularly in vegetative characteristics, is evident in both fossil and extant specimens. Because of this it is concluded that it is not possible to construct a list of constant criteria for the identification of the four genera. Confident identification can only be made when a large suite of the material is at hand and when it is judged on the basis of many criteria and compared to extant material. Implicit in this conclusion is the concept that the fossil material being dealt with spans a time period of over 60 million years, and that the evolutionary changes possible in this time period must be taken into consideration. An excellent example of this possible evolutionary variation is the genus *Parataxodium* Arnold and Lowthar (1955). While tentatively placed in synonomy with *Metasequoia occidentalis* in this thesis pending further examination of the material, it shows a range of characteristics that overlap both *Metasequoia* and *Taxodium*.

In the past, identification of these genera has often been made on relatively few specimens showing ill-defined characteristics. In an attempt to avoid the possible paleoecological and phytogeographical errors based on such identification, the new genus, *Taxodiophyllum*, has been

FIGURES 80-85.

Fig. 80. Specimen of extant *Taxodium dubium* from the University of Alberta greenhouses, showing a deciduous shoot with leaf arrangement either subopposite or opposite. X 1.5

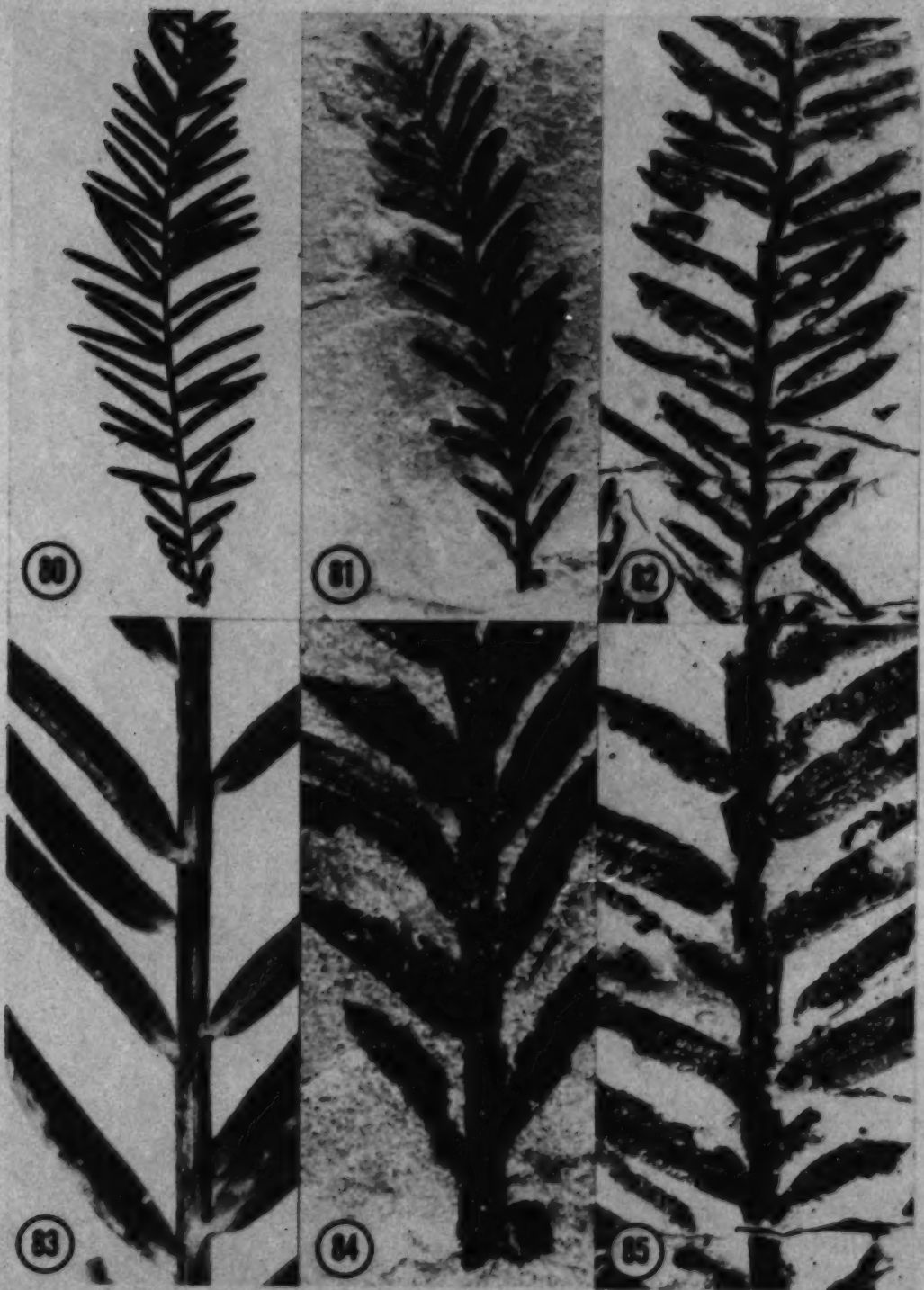
Fig. 81. Specimen S1040 - holotype of *Taxodiophyllum cordillarum* sp. nov. from Genesee, Alberta. X 3

Fig. 82. Specimen P67.1.145 - a deciduous shoot of *Glyptostrobus nordenskioldii* from the tuff horizon showing pronounced taxodioid leaves; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 2

Fig. 83. Enlarged view of Fig. 80 showing the subopposite arrangement of some leaf pairs and the parallel nature of the leaf base in reference to the shoot axis. X 4

Fig. 84. Specimen S1040 - enlarged view of Fig. 81 showing the position and nature of the leaf bases. X 5.5

Fig. 85. Specimen P67.1.145 - enlarged view of Fig. 82 showing leaf attachment. X 4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proposed for specimens of uncertain affinities. While admittedly artificial, this genus is hoped to provide a place of assignment (either temporary or permanent) for limited or questionable taxodiaceous remains.

Class: Angiospermae

Sub-class: Dicotyledonae

Family: Cercidiphyllaceae

Cercidiphyllum sp. (Figs. 86, 87)

Description - Twelve specimens which could be assigned with confidence to the genus were collected. Identification was based on the presence and position of the three major primary veins, general leaf shape, nature of the margin and the presence or absence of glands. Comparison with the excellent collection of *Cercidiphyllum* from the Genesee locality supported the identification.

Leaves ranged from 2.0 - 7.5 cm in maximum length and from 1.7 - 7.8 cm in maximum width. Of the 12 specimens, two exhibited a cordate base, while others ranged from cuneate to obtuse.

Discussion - An exhaustive study of *Cercidiphyllum* by Chandrasekharam (1972) resulted in division of known fossil material (of Cretaceous or Paleogene age) into three species. Much of this work was made possible by the excellent preservation encountered in specimens of *Cercidiphyllum* from the Genesee locality. Unfortunately, material

assignable to this genus from the Smoky Tower locality lacked this remarkable preservation, and many of the criteria for specific assignment used by Chandrasekharam were unavailable to the author. In a personal communication, Dr. Chandrasekharam expressed the opinion that the majority of the specimens probably represented *Cercidiphyllum flexuosum* (Hollick) Chandrasekharam based on the arcuate nature of the primary veins and on the margin (Fig. 86). However, certain specimens were more likely representative of *C. geneseviánum* Chandrasekharam (Fig. 87) and it was also possible that the third recognized species, *C. cuneatum* (Newberry) Chandrasekharam was also present. In the final analysis, however, he agreed with the author that assignment beyond the generic level was undesirable because of the poor preservation and the paucity of specimens.

Family: Platanaceae

Platanus raynoldsii Newberry (Figs. 88-91)

Description - Leaves found at the Smoky Tower locality range from ovate in the smaller specimens to tri-lobed in the larger ones (Fig. 88). The margin is undulate with glands observable on some of the teeth. The base, when present, ranges from truncate to cordate with 2-3 small lobes occasionally observable at the base (Figs. 90, 91).

Discussion - The 32 specimens which were collected from the Smoky Tower locality and assignable to this genus make this the angiosperm genus with the highest recorded frequency at

the locality. While no entire specimens were collected, the characteristic lobing combined with the typical major venation and size allowed the specimens to be assigned to the genus with confidence. Brown (1962) placed a large number of specimens of different genera and species in synonomy with *P. raynoldsii*. The major leaf characteristics (i.e. venation, margin, and major lobing) correspond closely in the Smoky Tower material with that figured by Brown (1962) and also later by Chandrasekharam (1972). It is interesting to note, however, that the basal lobes prominent in some specimens from the Smoky Tower locality (Figs. 90, 91) are not mentioned or figured for this species by Brown. The only specimens figured by Brown (1962) for the genus *Platanus* which do show the basal lobing feature were placed by him in the species *P. nobilis* Newberry. In his descriptions and discussions of the two species, however, he fails to mention whether he considered this a distinguishing feature. Furthermore, he did figure a specimen of the extant *Platanus occidentalis* Linneaeus (Brown, 1962, Plate 29, Fig. 2) which illustrates the basal lobing, but did not mention it as differing from *P. raynoldii* in this characteristic.

In discussions with Professor H. MacGinite of the University of California, Berkeley, in December, 1972, the opinion was put forth by that worker that the fossil species of the genus *Platanus* are in need of revision based on studies of the variation observable in the extant species

FIGURES 86-91.

Fig. 86. Specimen S1640 - *Cercidiphyllum* sp. showing irregular serrations, palmate major venation and irregular tertiary venation. X 1.3

Fig. 87. Specimen P67.1.07 - *Cercidiphyllum* sp. showing palmate major venation and definite marginal glands; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 1.7

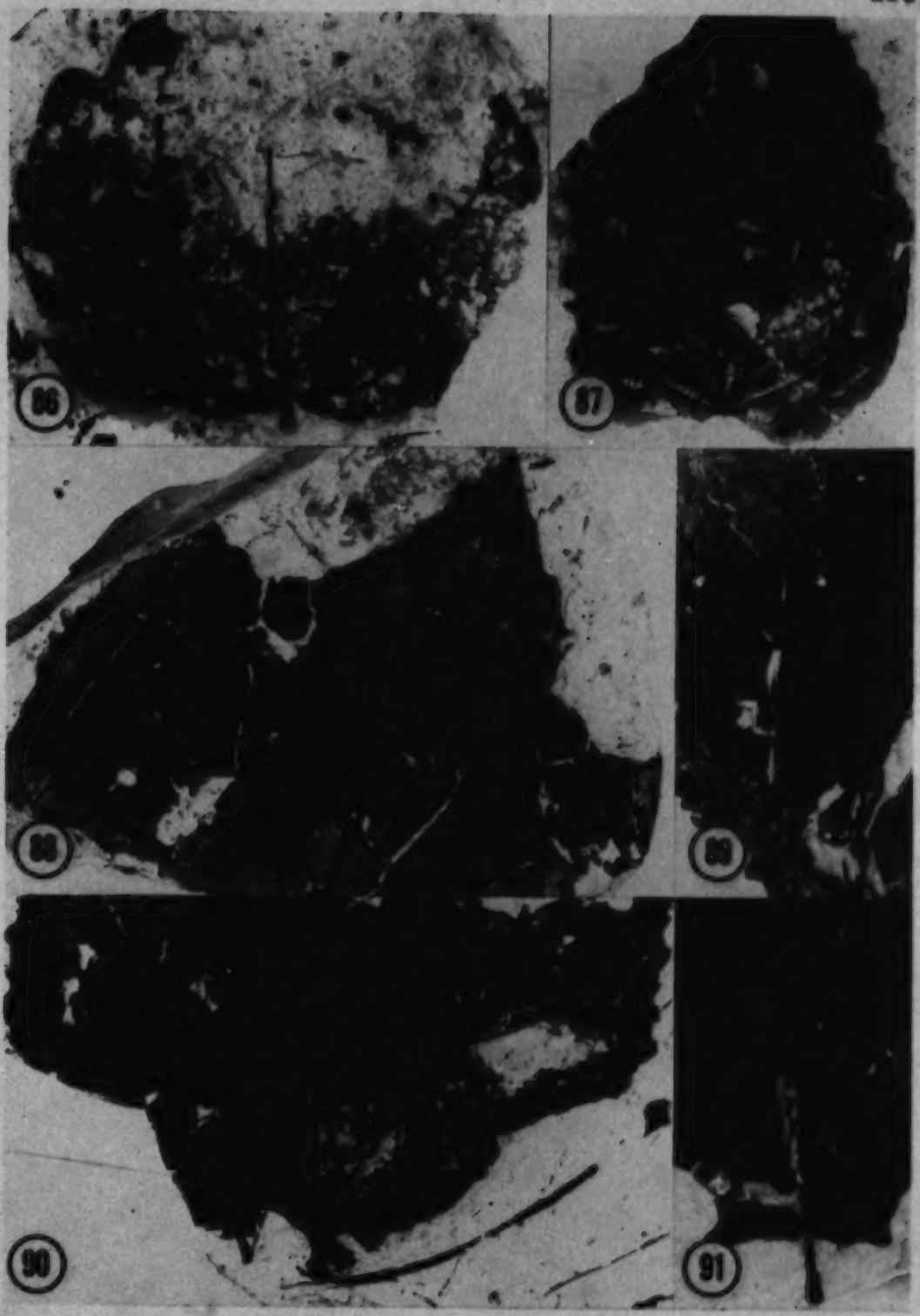
Figs. 88-91. *Platanus raynoldsii* Newberry from the tuff horizon.

Fig. 88. Specimen S1646B - shows three major apical lobes typical of a mature leaf of the taxon. X 0.7

Fig. 89. Specimen S3046B - shows central area of a large leaf with an *Equisetum* rhizome growing through it. X 1

Fig. 90. Specimen P67.2.27 - shows the base of a large leaf with several basal lobes near the petiole; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X .85

Fig. 91. Specimen S2775 - base of leaf showing distinct basal lobes. X 1.5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91

of the genus. As such a study was not within the scope of this thesis, assignment of the Smoky Tower specimens of *Platanus raynoldsii* is made with some hesitancy. As is pointed out by Chandrasekharam (1972, p. 138) *Platanus raynoldsii* seems to agree in its general characteristics with the extant *P. cuneata* Willd. Until more detailed comparisons of *P. cuneata* and *P. occidentalis* in all their variants are made with the fossil material, the status of fossil species of *Platanus* remain uncertain.

Family: Ulmaceae

Zelkova sp. (Figs. 92-94)

Description - The leaves range in length from 3.0 - 6.5 cm and in maximum width from 2.0 - 4.5 cm. The margins show doubly serrate teeth (Fig. 93) and in general the leaves display craspedodromous secondary veins and have a generally asymmetrical outline. All specimens encountered appear coriaceous and show a definite irregularity in the displacement of secondary veins.

Discussion - The definite ulmaceous affinities of the specimens from the Smoky Tower locality are shown by the nature of the teeth (acuminate on both basal and apical sides), by the craspedodromous secondary veins, and by the slight asymmetry of the leaf shape. The 16 specimens collected which are referable to this genus make it the second most common angiosperm leaf fossil encountered in the tuff horizon.

Differentiation between fossil representatives of *Ulmus* and *Zelkova* is often difficult. The general characteristic most often used is the nature of the marginal serration (Brown, 1962). *Ulmus* usually displays regularly doubly-serrate teeth, while *Zelkova* has uniserrate teeth with occasional double serrations. The Smoky Tower material generally displays both single and double serrations on any given specimen, and therefore fits best with the genus *Zelkova*. A comparison with other fossil ulmaceous specimens described in the literature shows that the best comparisons can be made with *Zelkova oregoniana* (Knowlton) Brown (Becker, 1961, Plate 18, Figs. 13-18). Favorable comparisons may also be drawn with the extant *Zelkova serrata* Makino (Brown, 1962; Becker, 1961) which is restricted in its distribution to eastern Asia.

Photographs of Fig. 92 and of other specimens were sent to Dr. J. Wolfe, United States Geological Survey, for an opinion. In his reply, Dr. Wolfe stated:

> "From the illustration, your leaf appears to be somewhat more primitive than *Zelkova*, in that the secondary veins are more irregularly spaced.... Your leaf represents (insofar as I can tell without seeing fourth and higher order venation) either an extinct genus or a primitive member of *Zelkova*."

Because of the lack of preservation of higher orders of venation, as mentioned by Wolfe, and also because of the paucity of specimens, it is the opinion of the author that it would be unwise to consider creation of a new genus or even specific assignment. Thus, the ulmaceous remains from

the Smoky Tower locality will be identified as *Zelkova* sp. until such time as more definitive material is found or more definite distinguishing criteria are established.

Incertae sedis

The positive affinities of the specimens shown in Figs. 95-102 are at present unknown. They will be discussed separately by figure number.

Fig. 95

In addition to the figured specimen, four others were recovered from the Smoky Tower locality. While the structure is obviously reproductive, preservation is too poor for positive identification. The two most obvious possibilities are (1) that the specimens represent the cones of a *Lycopodium*-like plant or (2) that they represent the reproductive structures of amentiferous angiosperms. The first possibility is supported by the sporophyll-like appearance of the units attached to the main axis (Fig. 95, letter T). Their relationship to the axes and their shape is reminiscent of the sporophyll morphology of an extant *Lycopodium*. The lack of vegetative remains assignable to *Lycopodium* weakens this possibility, however. The second possibility, that of angiospermous affinities, is supported by the number of unidentifiable angiosperms represented by leaf remains which might possess this type of reproductive structure.

One structure was sacrificed by macerating a portion of it and making an acetate peel of the remainder. The

maceration yielded no spores or other helpful material, and the peel did not reveal any other distinguishing features. The maximum length of the specimens ranged from 2.5 - 5.5 cm which puts the structures well within reasonable size range for either a *Lycopodium* cone or a catkin.

Figs. 96, 98

Seven specimens of a similar nature were recovered from the locality. The figured specimen shows a branch with what appears to be one entire and one partial, naked spur shoot. The entire shoot is 42 mm long and 12 mm at its maximum width. The preservation of the partial shoot fragment on the same specimen (Fig. 98) shows detail that compares favorably with a specimen identified as a *Ginkgo* spur shoot by Becker (1969, Plate 5, Fig. 1). The presence of numerous *Ginkgo* leaves in the flora adds support to this possibility, but as no leaves were ever found attached, and as other conifers with possible spur shoots were present, no formal assignment could be made.

Fig. 97

This specimen represents the only definitely compound angiosperm leaf collected. Of the three leaflets shown in the figure, the one on the left is best preserved. It has a maximum length of 44 mm and a maximum width of 19 mm. The leaflets show pinnate venation, possess an entire margin, and are craspedodromous. Further detail could not be observed because of poor preservation.

FIGURES 92-95.

Figs. 92-94. *Zelkova* sp. from the tuff horizon, Smoky Tower locality.

Fig. 92. Specimen P66.8.68 - deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 3

Fig. 93. Specimen P66.8.68 - enlarged view of another leaf showing the double serrations on the right and the tertiary venation pattern; deposited in the Alberta Provincial Museum and Archives collection, Edmonton. X 5.6

Fig. 94. Specimen showing several related similar leaves; unnumbered specimen deposited in the private collection of Mr. B. Tiemons, Grande Prairie, Alberta. X 1.8

Fig. 95. Specimen S2757 - *Incertae sedis*; a reproductive structure similar to either *Lycopodium* (letter T shows upturned tip of one of the units, reminiscent of a *Lycopodium* sporophyll) or to an amentiferous catkin. X 2.8

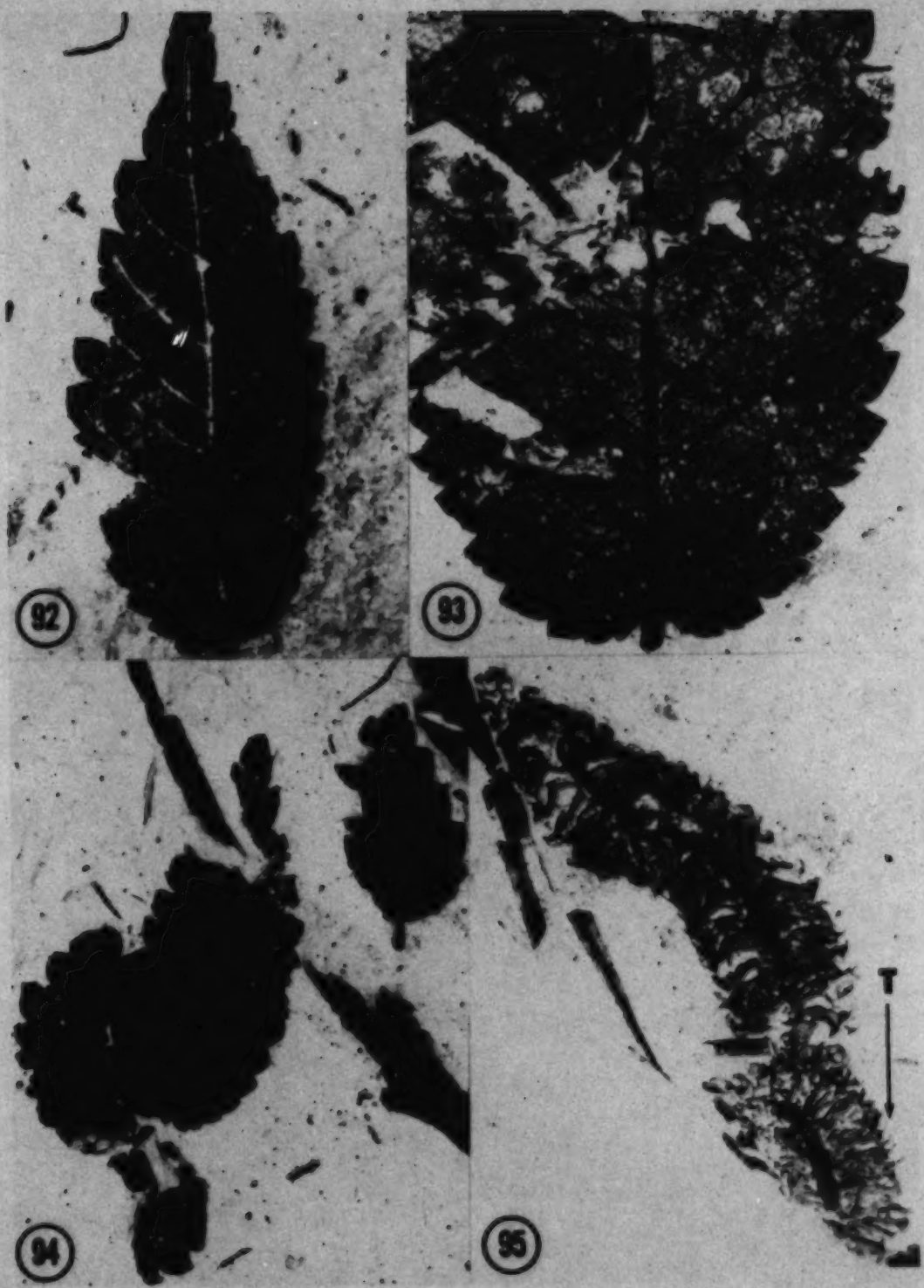
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Fig. 99

This specimen has a maximum width of 52 mm and an estimated maximum length of 75 - 90 mm. The venation is pinnate with strong craspedodromous secondaries with regularly looping tertiaries. The margin is coarsely dentate with large glands visible at the apex of each tooth. Five pairs of subopposite secondary veins are visible. Despite the good preservation shown by the portion of the leaf present, the absence of both the base and the tip makes identification impossible. It may be seen that the specimen was found in association with *Thujopposites interruptus*.

Fig. 100

This specimen represents the only complete, entire margined leaf recovered from the tuff horizon of the Smoky Tower locality. It has pinnate venation, with irregular secondaries which exhibit a craspedo-camptodromous disposition. The maximum length (including what appears to be a drip-tip) is 88 mm while the maximum width is 62 mm. In general this specimen is quite similar to one other entire margined leaf from the tuff horizon with the exception that the latter has regularly opposite secondary veins while this specimen has irregularly alternate ones.

Fig. 101

Three leaves similar to the figured specimen were recovered from the tuff horizon. All specimens show a definite cordate base, irregularly serrate dentition,

FIGURES 96-100.

Figs. 96-100. *Incertae sedis* from the tuff horizon, Smoky Tower locality.

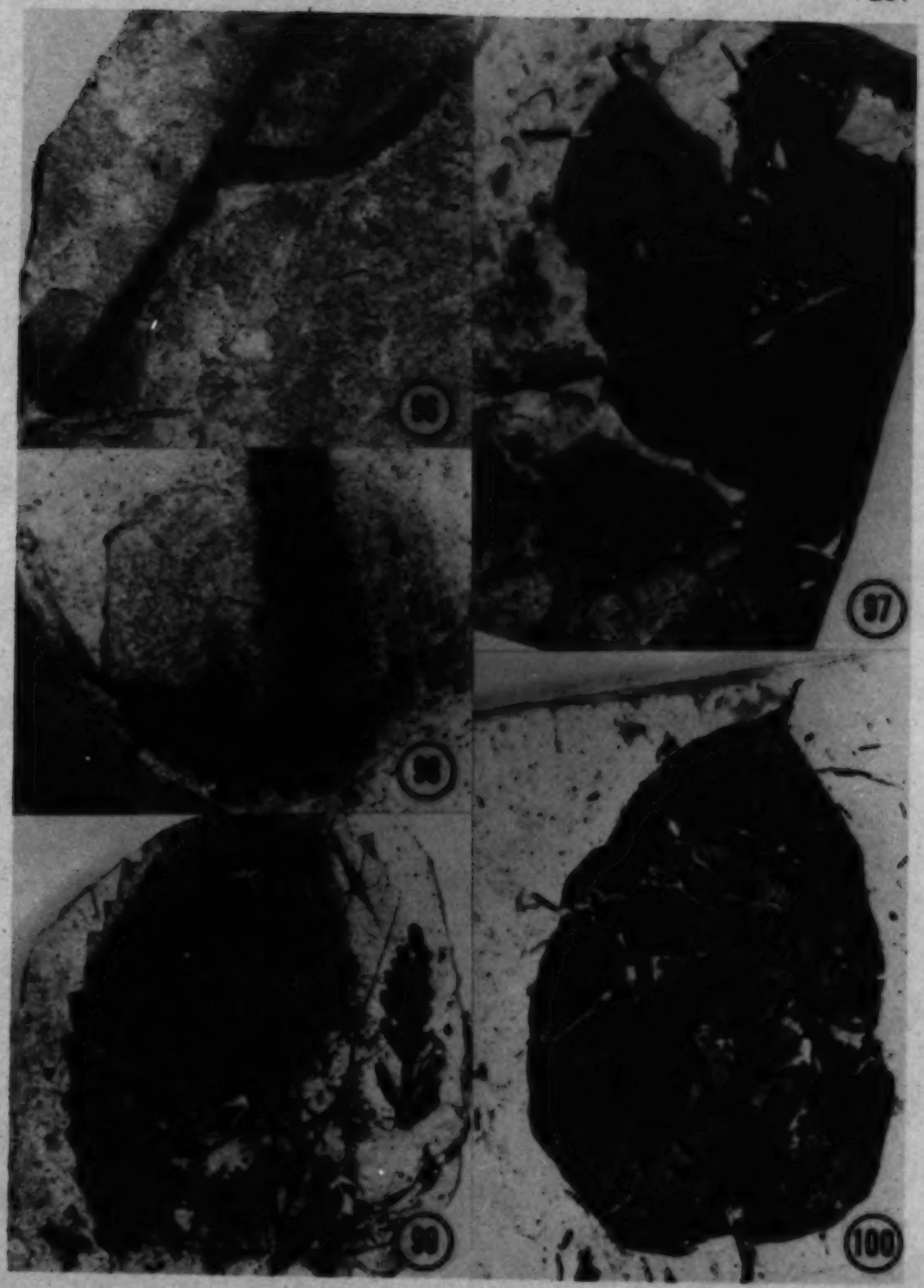
Fig. 96. Specimen S1835 - branch with two naked spur shoots; similar to specimen described as *Ginkgo* spur shoot by Becker (1969). X 1.4

Fig. 97. Specimen S3422A - compound angiosperm leaf showing an entire margin on each leaflet and nearly opposite, pinnate primary venation. X 1.7

Fig. 98. Specimen S1835 - enlarged view of Fig. 96 showing the tightly packed spiral of probable leaf bases. X 4

Fig. 99. Specimen S1944 - angiosperm leaf showing a serrate margin; twig of *Thujopposites interruptus* visible on the right. X 1

Fig. 100. Entire margined angiosperm leaf with a drip-tip; numberless specimen deposited in the private collection of Mr. B. Tiemons, Grande Prairie, Alberta. X 1.3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100

craspedodromous venation with regularly spaced secondaries and irregular tertiaries. The figured specimen has a maximum length of 82 mm and a maximum width of 66 mm which occurs approximately one-third of the distance from the base. All three specimens compare favorably with the genera *Vitis* and *Ampelopsis* of the family Vitaceae as figured by Brown (1962). However, a large enough suite of specimens was not present for definite identification, nor was preservation that good.

Fig. 102

Only one specimen of this nature was recovered. The leaf has a maximum width of 67 mm and a maximum length of 110 mm (excluding the short petiole). The margin is coarsely serrate and the venation pattern shows a strong mid-rib with alternate craspedo-camptodromous secondaries. The apices of the coarse marginal teeth appear glandular, and the apex of the leaf is elongated into what might be termed a drip-tip.

Siltstone Flora

Approximately five feet above the tuff bed containing the coniferous flora just described is a layer of siltstone 3-4 feet in thickness which contains another fossil flora (Text-Figs. 1, 2). Unlike the tuff flora, this one is composed primarily of angiosperm leaf remains and the remains of vascular cryptogams. The matrix is somewhat

FIGURES 101-104.

Fig. 101. Specimen S3434B - *Incertae sedis* from the tuff horizon; possibly belonging to the Vitaceae. X 1.25

Fig. 102. Specimen P67.1.61 - *Incertae sedis* from the tuff horizon. X 0.9

Fig. 103. Specimen S3892 - *Glyptostrobus nordenskioldii* (Heer) Brown from the siltstone horizon, site B; probable seed cones shown on the right of the specimen. X 1.25

Fig. 104. Specimen S3841 - *Azolla* sp. from the siltstone horizon. X 5

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darker, leaving slightly less contrast with the carbonized remains (Fig. 2) than found in the tuff horizon (Fig. 3). However, preservation is slightly better, with some tertiary and higher orders of venation being visible. The diversity of this flora was not realized until late in the study, and thus many angiosperm leaves, which may later prove present at the site in statistically significant quantities, are either omitted from this thesis or treated as *Incertae sedis* because of the small number of specimens collected. Following is a list of the genera collected, with the number of each variety placed in parentheses and the approximate percentage of flora following. Collecting indicated that the lateral distribution evident in the tuff horizon was not present in the siltstone horizon. However, the occurrence and deposition of *Equisetum* shown in the tuff horizon was also found here. Because of this and the large number of angiosperm remains not identified, the percentages of the various taxa in the flora calculated may not be truly representative in spite of the random distribution evident.

Class: Equisetinae

Family: Equisetaceae

Equisetum arcticum Heer (64) 29%

Class: Filicinae

Family: Salviniaceae

Azolla sp. (10) 4%

Incertae sedis (14) 6%

Class: Gymnospermae

Family: Taxodiaceae

Glyptostrobus nordenskioldii Heer (4) 0% (specimens found at site B)

Class: Angiospermae

Sub-Class: Monocotyledoneae

Incertae sedis (37) 16%

Sub-Class: Dicotyledonae

Family: Cercidiphyllaceae

Cercidiphyllum sp. (45) 20%

Family: Caprifoliaceae

Viburnum sp. (14) 6%

Family: Ulmaceae

Incertae sedis (15) 7%

Incertae sedis (20) 9%

Class: EQUISETINAE

Family: Equisetaceae

Equisetum arcticum Heer

Description - Specimens representing almost all organs associated with plants of the genus *Equisetum* were found in the siltstone horizon. Unlike the tuff horizon, the siltstone beds are rich in aerial remains as well as those belonging to underground portions of the plant. Numerous

detached leaf-sheaths (Fig. 105) were found as were sections of stem with the leaf-sheaths still in place (Fig. 106). Nodal plates collected exhibited dark areas in the position occupied by vascular bundles in extant plants (Figs. 108, 110). These dark areas varied in number from 13 - 17, with the most common number being 15 (Fig. 110). Some internodal cross sections were also preserved, and these have what appeared to be 10 areas representing vallecular canals (Fig. 109). Underground portions of axes were collected which have attached tubers (Fig. 107). The largest number of tubers observed was 10, with the average being 7.

Numerous structures were found detached, yet associated with *Equisetum* remains, which bear a striking resemblance to old, dried strobili (Fig. 111). These structures exhibit 8-20 pairs of what appear to be peltate sporangiophores (Fig. 111, letter P). Peeling and maceration techniques failed to yield additional evidence for this interpretation or to shed any light on the identity of the specimens. As none have actually been found attached to *Equisetum* vegetative remains, the interpretation will have to remain tentative.

Discussion - Earlier in the chapter, under the heading "Tuff Flora", the parameters of *Equisetum arcticum* Heer were discussed in detail. As with the specimens from the tuff horizon, those from the siltstone fit within Heer's diagnosis in regard to general size, shape, and tuber

FIGURES 105-111.

Figs. 105-111. *Equisetum arcticum* Heer from the siltstone horizon, Smoky Tower locality.

Fig. 105. Specimen S1969B - unattached leaf-sheaths. X 1.8

Fig. 106. Specimen S3801B - aerial axis showing ribbing and an attached leaf-sheath with 9 teeth. X 2.5

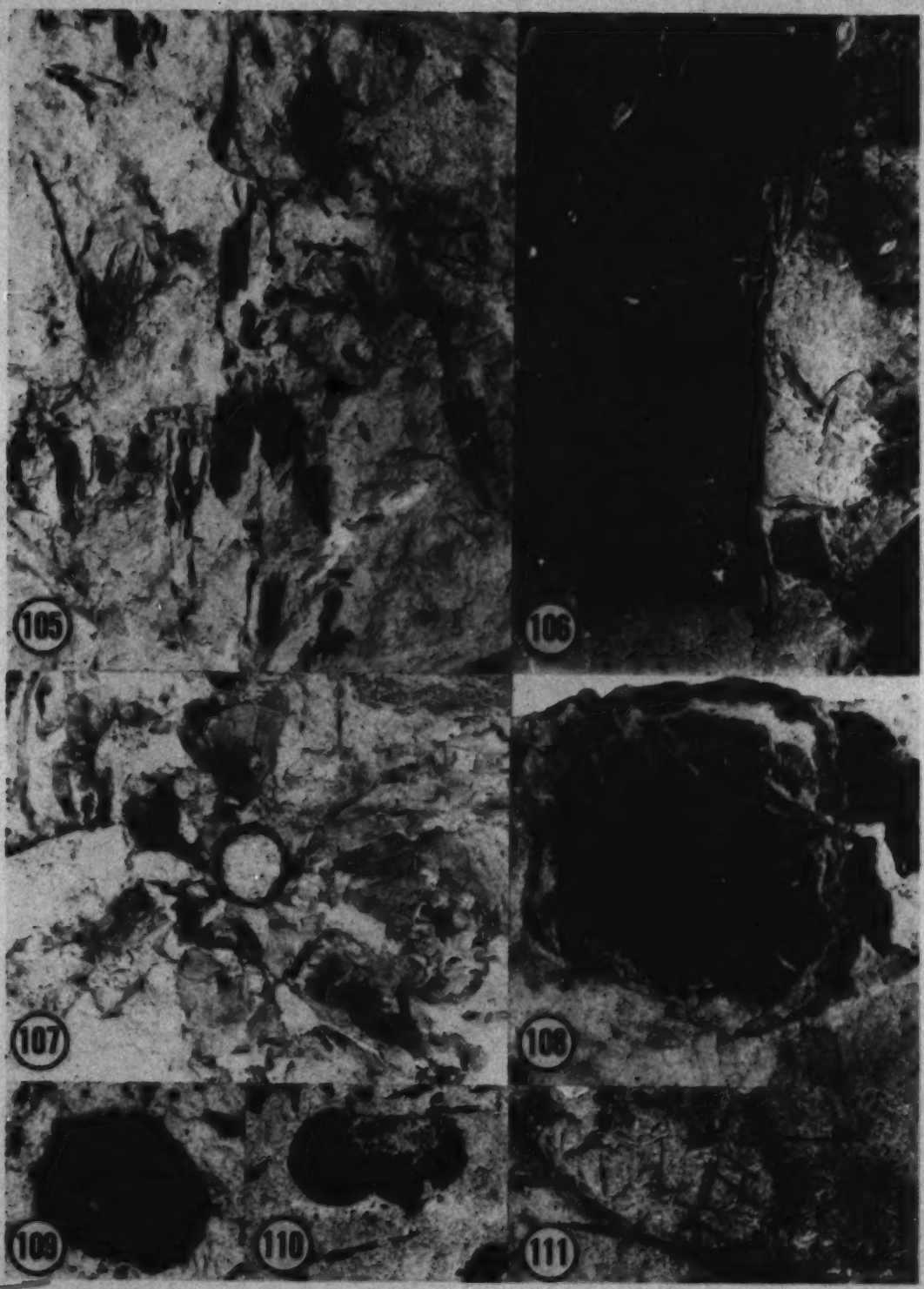
Fig. 107. Specimen S3224 - cross section of a rhizome node showing portions of 7 tubers. X 1.8

Fig. 108. Specimen S3891 - nodal plate showing the apparent position of 18 vascular bundles. X 5

Fig. 109. Specimen S3725B - internodal cross section apparently showing 13 valecular canals and a pith cavity. X 8

Fig. 110. Specimen S3803A - double nodal plate with the left plate showing the apparent position of 15 vascular bundles. X 4

Fig. 111. Specimen S3798A - possible shrivelled strobilus showing peltate sporangiophores (letter P). X 2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morphology. While features not encompassed in Heer's diagnosis are present in the material from the siltstone horizon (e.g. nodal anatomy, possible reproductive structures), they are not taxonomically significant enough to warrant creation of a new species or emendation of Heer's diagnosis for *E. arcticum*.

It is interesting to note that like the *Equisetum* in the tuff horizon, underground axes are found running at a variety of angles to the bedding plane in the siltstone horizon. This would appear to indicate growth after initial deposit of some of the sediments involved. This concept is discussed more thoroughly in another portion of the text (pp

Class: FILICINAE

Family: Salviniaceae

Azolla sp. (Fig. 104)

Description - Fragmented stems ranging from 2 - 4.5 cm in length, branching pinnately, and possessing bilobed leaves were collected from the siltstone horizon. The lobes of the leaves average 2.0 mm in length and just over 1.0 mm in width. The remains were found in overlapping patches, and thus individual leaf shapes and sizes were not determinable for much of the material. No reproductive structures were found.

Discussion - None of the 10 specimens found showed either

micro or megaspore complexes as were found in comparable material from Genesee, Alberta (Chandrasekharam, 1972, pp 25-27). The Genesee material was placed in the expanded species *Azolla schopfii* which had originally been created for reproductive material. Although the Smoky Tower vegetative material is very similar in size and shape to the vegetative portions of the Genesee material, the lack of reproductive material makes it impossible to assign it to the same species. The Smoky Tower *Azolla* is therefore left as *Azolla* sp. until such time as reproductive structures are recovered or more vegetative details are obtained.

Incertae sedis

Description - Fourteen additional specimens definitely assignable to the Filicinae were recovered from the siltstone horizon of the Smoky Tower locality. They represent fragments of sterile fronds (Fig. 112) made up of from 5-13 pairs of primary pinnae, each consisting of 10-16 pairs of imbricated pinnules. The specimen shown in Fig. 112 illustrates the degree to which the pinnules overlap, and this, coupled with the coarseness of the matrix makes taxonomic identification very difficult. For example, it is impossible to say whether or not the pinna shown by the letter P in Fig. 112 is composed of pinnules or represents a single unit. The figured specimen has an over-all

maximum length of 9 cm and a maximum diameter (basal entire pinna shown) of 5.5 cm, which also represents the maximum length of a primary pinna.

Discussion - Identification of ferns on purely vegetative remains is often difficult. The material found in the siltstone horizon bears a distinct resemblance to the material collected at the Genesee locality (Chandrasekharam, 1972) and which was identified as *Woodwardia arctica* Heer. However, as Brown (1962) pointed out, this genus bears a close resemblance to the genus *Onoclea*, the only difference being the entire margin on the latter as opposed to a serrate margin on the pinnules of *Woodwardia*. While definite serrations appear on some of the specimens, others, such as the one figured, are difficult to interpret. It is even possible that more than one taxon is represented by the 14 specimens. Because of the general uncertainty surrounding their identification, the 14 specimens are placed in *Incertae sedis* pending the discovery of fertile material or more diagnostic sterile material.

Class: GYMNOSPERMAE

Family: Taxodiaceae

Glyptostrobus nordenskioldi Heer

Discussion - Four specimens were collected from the siltstone horizon at site "B" which are believed assignable to the genus *Glyptostrobus*. One specimen, shown in Fig. 103

has associated with it structures which appear to be glyptostroboid seed cones, thus strengthening the identification. These four specimens represent the only gymnosperm remains found in the siltstone horizon. It is interesting to note that these four, as well as specimens bearing fragments of *Equisetum*, were collected from a very limited outcrop of the horizon approximately 0.7 miles southeast of the main collecting area (site "B"). This could lead to interesting conclusions regarding the lateral variation of taxa within the siltstone horizon, but the limited nature of this other outcrop, in addition to the badly weathered condition of the specimens collected there, makes a more thorough study of this aspect impractical.

Class: ANGIOSPERMAE

Sub-Class: Monocotyledoneae

Incertae sedis

One of the most common members of the siltstone horizon flora, yet one of the most difficult to characterize and identify is a type of plant remain resembling broken leaves of an aquatic monocot such as *Typha*. Specimens are commonly found mixed with other genera, often with breaks or folds (Fig. 2, letter T). Of the 37 specimens collected, none showed either a proximal or a distal end, or gave any indication of tapering. The largest specimen recovered had a maximum length of 16.5 cm and a maximum width of 2.2 cm

with no more than a 0.2 cm variance in width throughout. The only detail preserved is dark lines running parallel along the length of the specimens in a position and of a size expected for the veins of an aquatic monocot.

As Becker (1969, p. 70) pointed out, without entire plants, fragments of fossil specimens of the genera *Typha*, *Phragmites*, and *Arundo* could be easily confused. Because of this, and the poor preservation thus far encountered in similar specimens from the siltstone horizon, the specimens are not assigned to a taxon at this time. Perhaps the most significant point is that all three genera mentioned by Becker are found as shore-line constituents of rather quiet bodies of water in the modern-day environment. Therefore, the presence of relatively large quantities of specimens possibly assignable to one of the three genera is consistent with the hypothesized depositional environment for the locality at the time of the formation of the siltstone horizon.

Sub-Class: Dicotyledoneae

Family: Cercidiphyllaceae

Cercidiphyllum sp.

The 45 specimens assignable to this genus are remarkably similar in over-all morphology. While their maximum length varies from 12 mm to 48 mm and the maximum width from 10 mm to 47 mm, the overall shape, venation, and marginal serration remains constant (Figs. 115, 116). One

of the few variations encountered was in the nature of the base. Some specimens show a definite truncation of the base with the inner primaries arising within the truncation (Fig. 116), while most show an obtuse or nearly cordate base (Fig. 115).

Personal communications with Dr. A. Chandrasekharam, who monographed the genus in 1972, indicated that that author agreed with the opinion that all 45 specimens are probably members of a single species. This differs from the *Cercidiphyllum* collected from the tuff horizon, which is thought by this author (and supported by Chandrasekharam) to contain two, and possibly all three of the species delimited in Chandrasekharam's 1972 work. As much of that work was based on extremely fine details of venation and statistics compiled from hundreds of specimens, it is not possible to confidently assign the more poorly preserved and scarcer Smoky Tower siltstone material to a given species, and identification has been left at the generic level.

Family: CAPRIFOLIACEAE

Viburnum sp.

Description - Of the 14 specimens collected from the siltstone horizon, 9 compared favorably with specimens shown by Brown (1962, Plate 64, Figs. 1-3, 5, 7-11, 6) and identified as either *Viburnum asperum* Newberry or as an ancestral form

of the species. The other five, while not directly comparable, are similar enough to the first 9 to be also included. The leaves range from ovate to spatulate in shape with a maximum length varying from 1.5 - 8.5 cm and a maximum width of 0.9 - 6.0 cm. All specimens are pinnately veined with a strong midrib. Venation is craspedodromous, with the margin being singly or doubly serrate.

Discussion - It is interesting to note that the specimen shown in Fig. 113 bears a striking resemblance to the specimen shown in Fig. 6, Plate 64, by Brown (1962) and labeled by him as being "a probable ancestor of *Viburnum asperum*". The slightly asymmetrical shape of this leaf gives a general appearance similar to many members of the Ulmaceae.

Photographs of the specimen shown in Fig. 117 were sent to Dr. J. Wolfe, United States Geological Survey, Menlo Park, California, for confirmation of identification. Dr. Wolfe (personal communication) stated that while he agreed that the specimens were identical with those historically identified as *Viburnum asperum*, it was his opinion that these specimens could well represent primitive members of the Ulmaceae based on the nature of the marginal teeth and the venation. Because of the opinion stated by Wolfe, and also taking into consideration the earlier observation on the specimen listed by Brown as ancestral, some doubt must be cast on the correctness of the placement of

specimens previously identified as *Viburnum asperum* in the genus *Viburnum* and perhaps even in the Caprifoliaceae. Only a thorough study of the leaves of the modern genera involved will allow a definitive statement to be made regarding the fossil specimens.

Family: Ulmaceae

Incertae sedis

If all the partial fragments probably assignable to this family were counted, this would be the commonest angiosperm taxon in the siltstone horizon at the Smoky Tower locality. As it is, the 15 specimens complete enough to make an identification are still not preserved well enough or in sufficient quantity to identify them at the generic level. The specimen shown in Fig. 114 has the typical ulmaceous venation and marginal teeth, and is very similar in appearance to a specimen figured by Becker (1969, Plate 21, Fig. 11b) and identified as *Zelkova ungeri* Kovats. Other specimens illustrated by Becker in the same plate are identified as other species of *Zelkova* and *Ulmus*. The close similarity of all of these specimens makes it impractical to assign the Smoky Tower siltstone specimens to a definite genus and species until a larger collection with perhaps better preservation is at hand.

Discussion - While it may be seen that relatively few definite identifications were made on the siltstone flora

FIGURES 112-117.

Fig. 112. Specimen S3733A - unidentified fern from the siltstone horizon; letter P indicates area where it is impossible to distinguish pinnae from pinnules. X 1.8

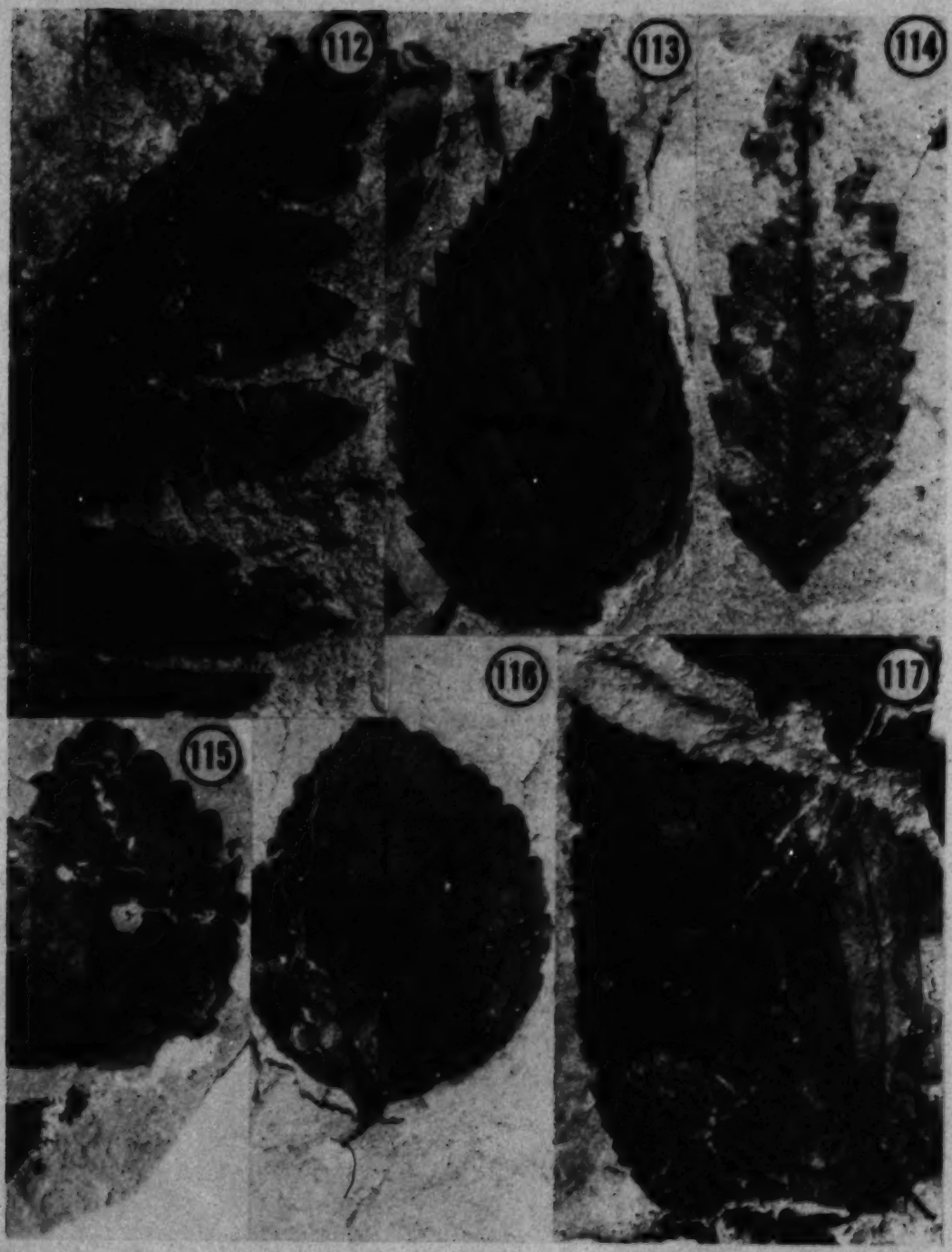
Fig. 113. Specimen S3806 - enlarged view of Fig. 2 showing a probable *Viburnum* leaf. X 4

Fig. 114. Specimen S3250A - unidentified ulmaceous leaf from the siltstone horizon. X 4

Fig. 115. Specimen S3058 - *Cercidiphyllum* leaf (possibly *C. flexuosum*) from the siltstone horizon; upper left portion of the leaf shows particularly good higher orders of venation. X 2

Fig. 116. Specimen S3252 - *Cercidiphyllum* leaf (possibly *C. flexuosum*) from the siltstone horizon; illustrates a variety with a truncated base in which major primary veins originate. X 2.5

Fig. 117. Specimen S3739A - probable *Viburnum* leaf from the siltstone horizon. X 1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from the Smoky Tower locality, the general differences between it and the tuff flora are nonetheless striking. A dominantly coniferous flora has been replaced in a relatively (geologically) short period of time by a dominantly angiospermous flora. Though not yet formally identified, it would appear that a more diverse flora is present in the siltstone horizon. It is hoped that further collection and a thorough comparative study of the comparable extant species will shed more light on the complexity of this flora. The possible significance of the differences between the siltstone flora and the tuff flora will be discussed in the concluding chapter.

Microflora

The numerous coal seams encountered at the Smoky Tower locality were all subjected to various techniques (pp 10-16) in an attempt to obtain microfossils for study and correlation with the megafloras. Particular attention was paid to those seams lithologically closest to the beds containing the fossil megafloras, and of these one in particular (Text-Fig. 2, Coal #2) yielded well preserved microfossils.

A thorough palynological study was not one of the major objectives of this thesis. Therefore, only the most typical and stratigraphically significant palynomorphs encountered are figured, and only a superficial taxonomic treatment is given them. Prior to the examination of the

fossil palynomorphs, representative pollen of the extant counterparts of the megafloral elements were examined. Subsequent study of the fossil pollen and spores showed almost a zero correlation between pollen types of the macrofloral elements and the fossil pollen types actually encountered. Photographs of the major palynomorph types encountered were sent to Dr. S.K. Srivastava, Chevron Oil Field Research Company, for identification. Unless specifically stated, all tentative identifications made in this thesis represent the mutual opinions of Dr. Srivastava and the author.

Following is a list of the palynomorphs with their relative frequencies (percentages). For this study a total of fifty fields from five different microscope slides was studied.

Laevigatosporites sp. (32%)
Lycosporites sp. (6%)
Tricolpites sp. (9%)
Aquilapollenites sp. (2%)
Engelhardtioidites sp. (9%)
Bisaccate grains (21%)
Miscellaneous (21%)

Laevigatosporites sp.

This genus is considered by many to be a catch-all taxon for both well preserved monolete grains and also many other morphs whose exines have been altered in some artificial manner. The two figured specimens (Figs. 124, 125) show the typical reniform shape with the single aperture. While this type of spore is found in some

groups of ferns, no taxonomic conclusions may be drawn from the fossil specimens. Although this genus represents the most frequent microfossil encountered in the coal sample, the possible artificiality of the genus makes it significance negligible.

Lycosporites sp.

As the name implies, this fossil spore bears a great similarity to the spores of extant *Lycopodium*. Particularly diagnostic is the outer membranous appearing portion of the exine. Presence of *Lycopodium*-like spores would become much more significant should the reproductive structures (Fig. 95) from the tuff flora prove to be identifiable as *Lycopodium*. The spore shown in Fig. 119 shows a suture of much the same shape and dimensions of that found in extant *Lycopodium* spores.

Tricolpites parvus Stanley

As the name suggests, this is a morphological genus based on the obvious tricolpate nature of the *palynomorph* (Fig. 120). The species was erected by Stanley (1965) and is common in uppermost Cretaceous and Paleocene microfloras. No definite correlation with an extant taxon is suggested.

Tricolpites vulgaris (Pierce) Srivastava

Only three grains assignable to this species were

observed in the fields counted. The generic designation is again obvious, while this particular species is identified on the basis of its larger size and less pebbled exine (Fig. 121). Srivastava (1969) found this to be a common angiosperm grain in the Maestrictian deposits of Alberta, but the species also commonly ranges into the Paleocene.

Aquilapollenites echinatus (Mschedlishvili) Rouse and Srivastava

Seven specimens referable to this taxon were recovered from the #2 coal seam (Text-Fig. 2) at the Smoky Tower locality. Identification was made by Dr. S.K. Srivastava (personal communication). However, comparison of illustrated specimens (Rouse and Srivastava, 1972, Fig. 48) with the Smoky Tower material (Fig. 118) has led the author to agree with Srivastava's identification. As Rouse and Srivastava indicate, this species is found in Cretaceous-Paleocene boundary sediments. Its affinities are unknown.

Engelhardtioidites teniupolus (Anderson) Srivastava

This genus and species were revised by Srivastava (1972) based on specimens found in Paleocene deposits in Alabama. The major feature differentiating it from other similar triporite grains (e.g. *Momipites*) is the lack of prominent, protruding lips around the pores (Fig. 122). The suggested taxonomic affinity is to *Engelhardtia*, a genus

in the Juglandaceae found in south-eastern Asia and Central America.

Bisaccate grains

While making up a large portion of the microflora, bisaccate grains are difficult to identify, and thus neither Srivastava or the author made an attempt at generic or specific identification. The specimen shown in Fig. 123 is probably assignable to *Podocarpites*, and is relatively infrequent in the coal seam studied. Most of the specimens making up the 21% of the flora which is bisaccate are probably assignable to genera of the Pinaceae.

Discussion - All specimens recovered which were identifiable at the species level have ranges extending across the Cretaceous-Paleocene boundary. It is the opinion of Srivastava (personal communication) that the flora probably represents a stratum comparable to the *Wodehousea spinata* Zone (Srivastava, 1970) above the Kneehills tuff. This opinion is based on the abundance of *Engelhardtioidites teniupolus* and the presence of *Aquilapollenites echinatus*, which is not known to occur above this zone. The obvious lack of the nominal taxon, *Wodehousea spinata* weakens this opinion. While the well log for the Smoky Tower locality does not show the Kneehills Tuff horizon, making it impossible to stratigraphically prove the correlation, the age suggested by this position is not inconsistent with the

FIGURES 118-125.

Fig. 118-125. Spores and pollen grains from Coal #2 (Text-Fig. 2) at the Smoky Tower locality, Alberta.

Fig. 118. *Aquilapollenites echinatus* from slide S10-301. X 2660.

Fig. 119. *Lycosporites* sp. from slide S10-303. X 1850.

Fig. 120. *Tricolpites parvus* from slide S10-301. X 3100.

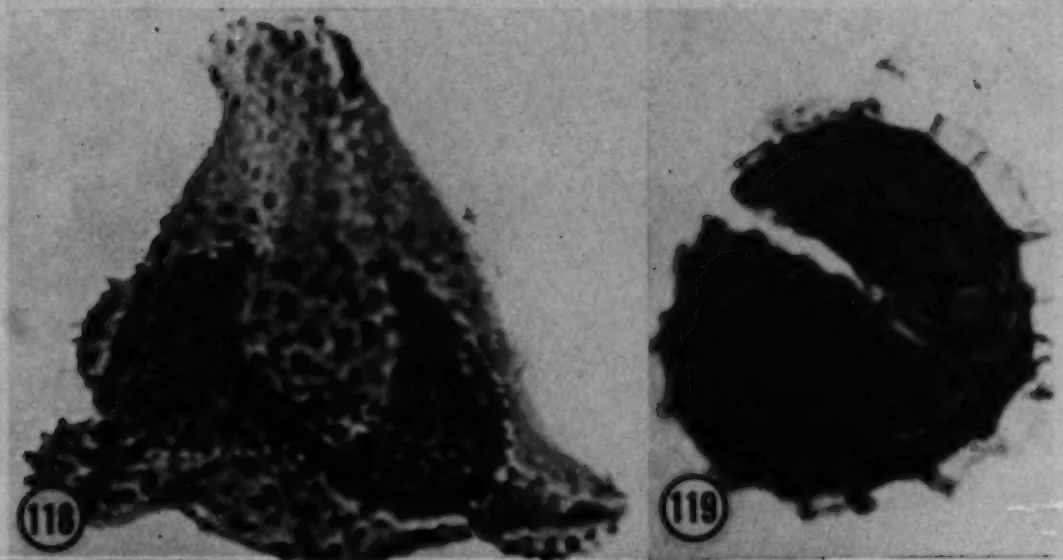
Fig. 121. *Tricolpites vulgaris* from slide S10-306. X 2350.

Fig. 122. *Engelhardtioidites teniupolus* from slide S10-302. X 1350.

Fig. 123. *Podocarpites* sp. from slide S10-305. X 720.

Fig. 124. *Laevigatosporites* sp. from slide S10-301. X 1100.

Fig. 125. *Laevigatosporites* sp. from slide S10-301. X 1100.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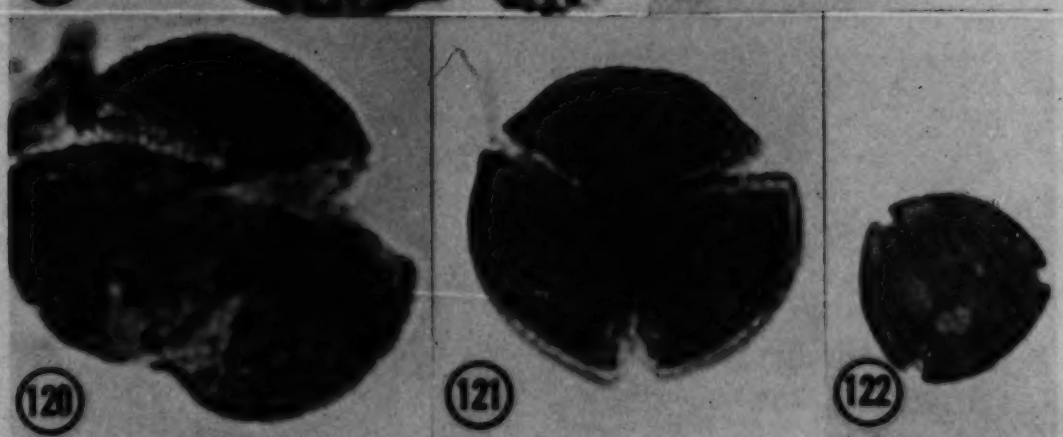
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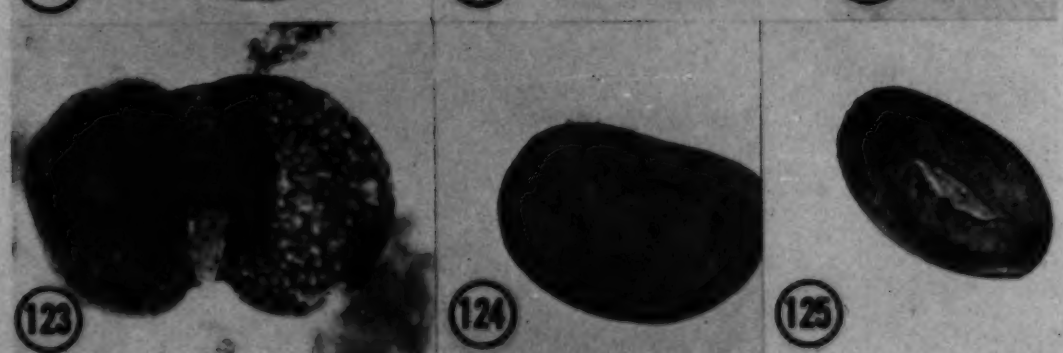
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information at hand on the age of the Smoky Tower strata.

Molluscan Fauna

In addition to the flora already discussed, the siltstone horizon (Text-Fig. 2) also contains a limited gastropod fauna. With major assistance from Dr. C. R. Stelck, Department of Geology, University of Alberta, tentative identifications were made for the specimens collected. Identifications were based on the descriptions and illustrations found in works on similar freshwater faunas (Russell, 1929, 1932, 1964, 1967; Tozer, 1956; Henderson, 1935). Among specimens examined, ones comparable to the following taxa were tentatively identified: *Lioplax nebrascensis*, *Valvata filosa*, *Oreohelix rotundata*, *Reesidella protea*, *Physa canadensis*, *Sphaerium fowleri*. None of these taxa have extremely restricted ranges, and all are found in strata of an age comparable with the Paleocene age assigned to the Smoky Tower locality and discussed in the next chapter. Many of the specimens were badly crushed, and as the identifications are only tentative, no specimens are figured within the thesis.

In addition to the siltstone fauna, the blocky sandstone just below this horizon (Text-Fig. 2) was found to contain pelecypod remains. These were comparable to *Unio stantoni* and are also known to occur in Paleocene strata.

Conclusions - The strata of the Smoky Tower locality have

yielded two distinct macrofloras, a molluscan fauna, and at least one microflora. The identifications of these assemblages, as discussed in the preceding pages, provide evidence for various stratigraphic and paleoecological conclusions which will be more thoroughly discussed in the final chapter.

CHAPTER 5

COMPARATIVE FLORISTICS AND AGE OF THE FOSSIL BEDS

Comparison of Smoky Tower Megafloras - From the systematic treatment in the preceding chapter, the two megafloras at the Smoky Tower locality can be seen to overlap very little in gross composition. For the sake of comparison, the elements identifiable to genera from each of the horizons are listed below:

Tuff Horizon	Siltstone Horizon
Sciadopitophyllum	*Equisetum*
Metasequoia	*Azolla*
Glyptostrobus	*Glyptostrobus ?*
Thujopposites	*Cercidiphyllum*
Equisetum	*Zelkova* or *Ulmus*
Ginkgo	
Cercidiphyllum	
Platanus	
Zelkova	

The primary difference between the two floras is the striking abundance of coniferous remains in the lower tuff horizon and the lack of them in the siltstone horizon. The

4 *Glyptostrobus* specimens listed in the siltstone horizon were found at site "B" and their credentials as members of the major flora may be questioned.

Thus *Cercidiphyllum* and possibly *Zelkova* become the only arborescent genera found which are common to both horizons. Even this overlap is not as significant as it might appear at first. In the opinion of Dr. A. Chandrasekharam, two and possibly all three of the species of *Cercidiphyllum* proposed by him (1972) for the Genesee flora are present in the tuff horizon of the Smoky Tower locality. However, while quantitatively more abundant, the *Cercidiphyllum* remains from the siltstone horizon are systematically more restricted, probably representing only one species, *Cercidiphyllum flexuosum*.

Similarly, the ulmaceous remains of the siltstone horizon, while quantitatively much more frequent, are, in the opinion of Dr. J. Wolfe (personal communication) certainly not the same species as represented by the specimens of the tuff horizon, and probably an entirely different genus. Thus the only positive correlation of remains of arborescent plants between the two horizons is represented by *Cercidiphyllum flexuosum* and its identification is tentative.

Though *Equisetum arcticum* Heer is present in both horizons the variable position of its remains with respect to the bedding plane in each of the horizons would indicate that its deposition was probably secondary to that of the

major floras of the horizons. It is interesting to note, however, that while only underground portions of *Equisetum* are found in the tuff horizon, both underground and aerial portions are present in the siltstone. This would seem to support the hypothesis that a much slower rate of deposition of sediments occurred to form the siltstone layer. While the underground portions of *Equisetum* grew through the ash deposits which later formed the tuff layer, they probably did so after the ash deposition was complete, and thus no aerial portions are preserved in the tuff. Following similar logic, while the *Equisetum* in the siltstone layer grew after the initial deposition of some of the sediment and associated leaves (as indicated by the position of preservation relative to the other fossils and by the fact that several angiospermous leaf remains have been pierced by the *Equisetum* rhizomes) deposition of the same sediment must have continued, as aerial axes, leaf-sheaths, and possible reproductive structures are also preserved in the same horizon.

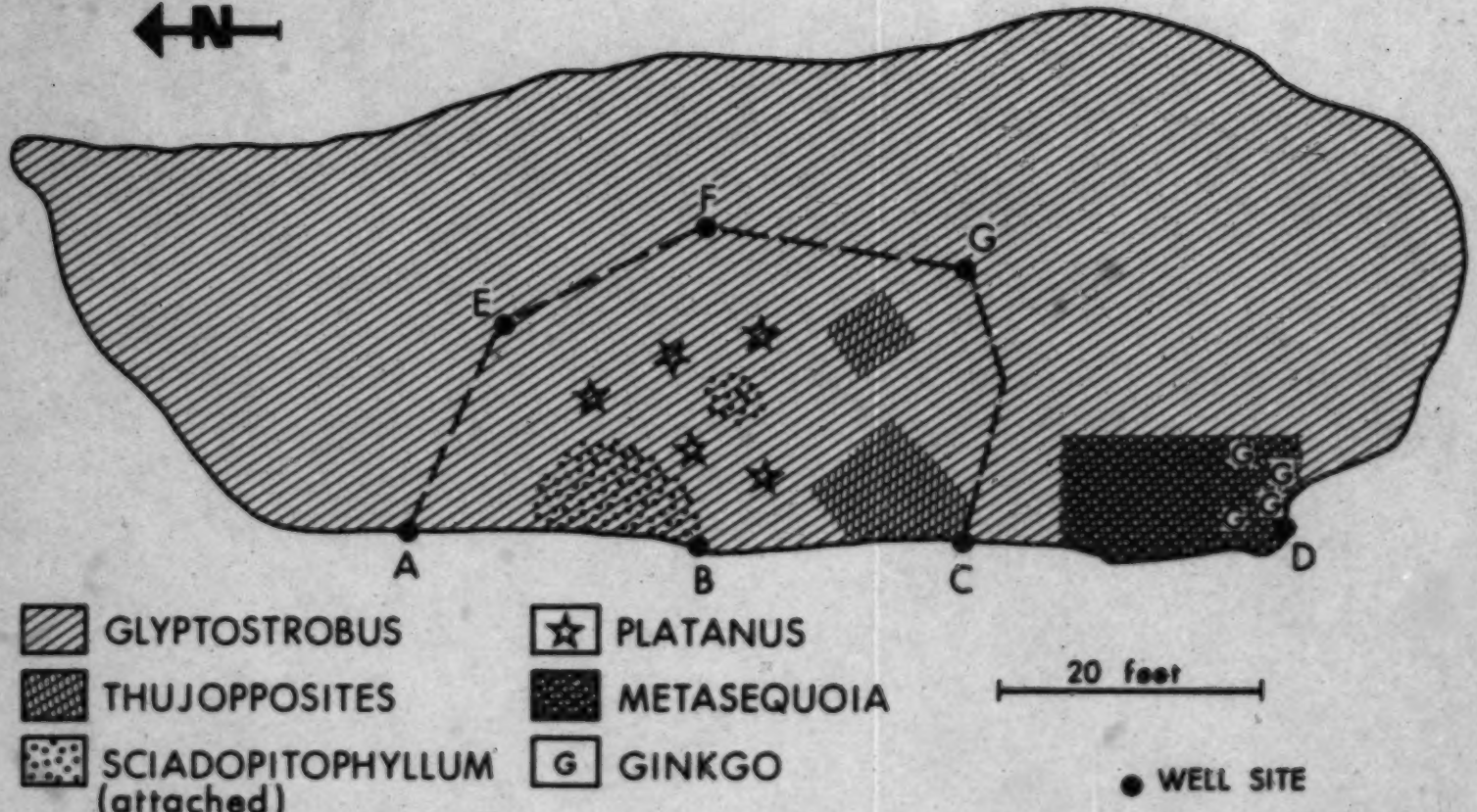
While the above observations may seem unrelated to a comparison of the two floras, they actually emphasize an important point. Based on these observations of *Equisetum*, it is highly probable that the entire flora represented by the tuff layer is far more restricted, both in the length of time of deposition and the area from which sediments were derived adjacent to the area of deposition than the siltstone horizon. In contrast, the upper siltstone horizon

may represent the center of a wide and long-term depositional area, and thus contain elements from ecologically different regions.

At first glance the lists of genera found in the two horizons would tend to indicate broad environmental changes, going from a predominantly coniferous forest to a habitat almost devoid of conifers and dominated by angiosperms. However, closer examination of the depositional factors which may have been in effect shows that the over-all environmental, and consequently floristic, conditions for the region may not have been as drastically different as the fossils preserved in each of the two horizons would indicate. Considering the possible differences in deposition it is possible that a comparison of the tuff flora with the siltstone flora may be similar to comparing the inhabitants of a microhabitat with those of the encompassing macrohabitat.

Lateral Distribution Within the Tuff Horizon - During the early stages of collecting at the Smoky Tower locality, when the tuff horizon was visible as a lateral band along the exposed hill face (Fig. 1, letter T), it became apparent that the various organ genera were located in specific areas within the outcrop, and not randomly distributed as might be expected. For example, after completion of the first exploratory collecting, it could be stated with confidence that collections made near the region designated A in Fig. 1 would contain primarily

specimens of *Thujopposites* and *Glyptostrobus*, while it could be said with equal confidence that collections made in the area of B (Fig. 1) would contain primarily detached needles of *Sciadopitophyllum* and *Glyptostrobus*. At D in the same figure, one could confidently expect to collect *Metasequoia* and the occasional *Ginkgo* leaf. Extensive collecting during the remainder of that season demonstrated that not only was there a distinct lateral restriction, but also as collections were made deeper into the hillside, various genera either expanded their range or declined. For example, collections made in mid-summer yielded the first attached specimens of *Sciadopitophyllum* in an area approximately 6 feet to the right of point A (Fig. 1). The enthusiasm accompanying this discovery resulted in extensive excavation in this area. It was soon discovered, however, that the area from which specimens were obtained was extremely limited, covering approximately 13 square feet. The tuff in this area yielded only 8 specimens. Because of this distributional phenomenon, permission was obtained to use a bulldozer in the area for more extensive collection. As a result of this excavation, a portion of the outcrop indicated by the letters A through C in Fig. 1 and A through G (excluding D) in Text-Fig. 6 was exposed. The distributions of various genera within this area may also be seen in Text-Fig. 6, with the corresponding area also shown in Figs. 126, 127.

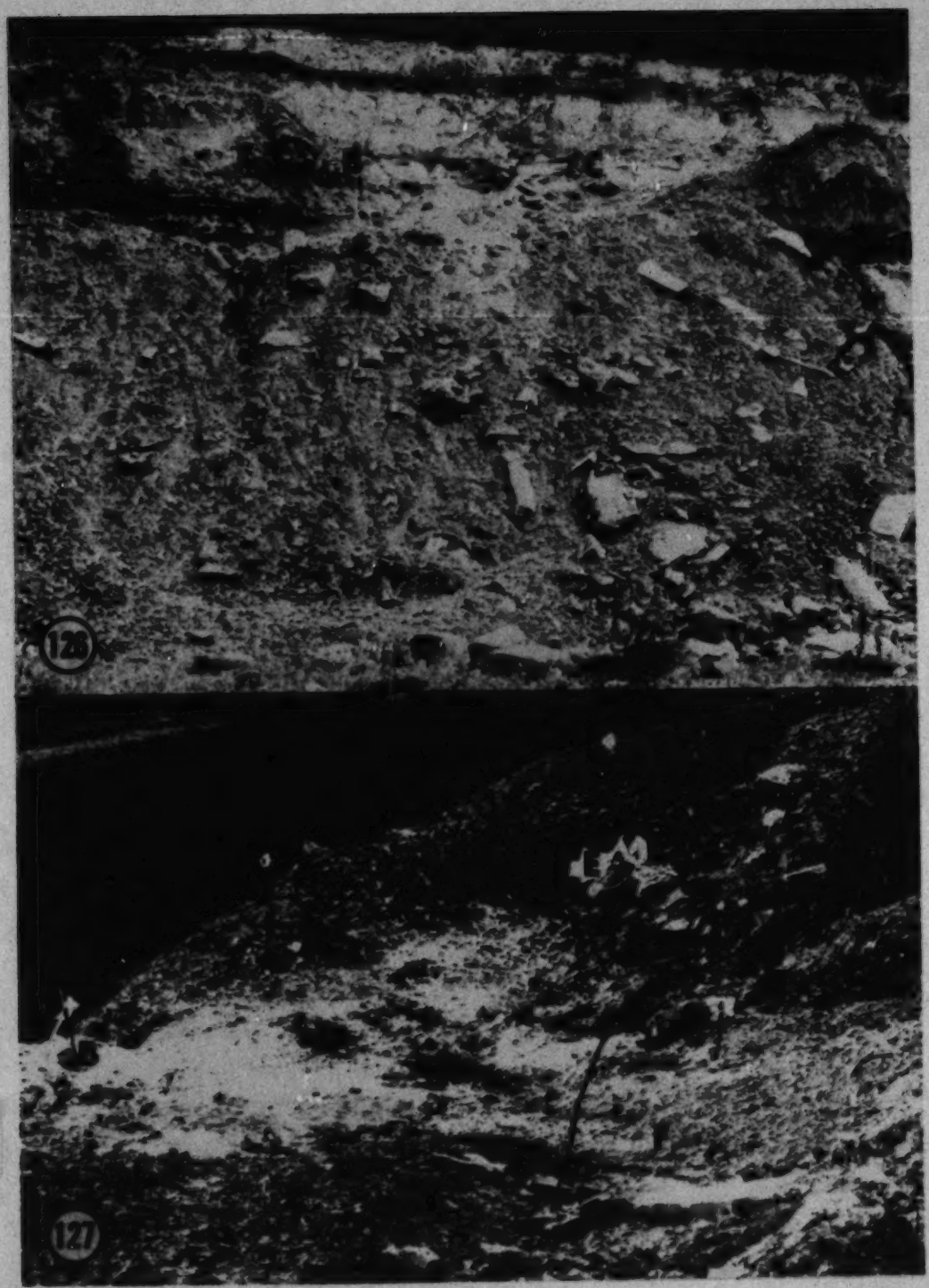


TEXT-FIGURE 6. Lateral distribution of plant fossils within the tuff horizon; area within the dashed lines (letters A-G) represents the bulldozed portion of the outcrop.

FIGURES 126-127.

Fig. 126. The Smoky Tower locality, facing east, after bulldozing operations. Letters A-D correspond to the same positions indicated by those letters in Figs. 1 and 127 and in Text-Fig. 6. All sediments overlying the tuff horizon were removed in the area between letters A and C. Coal #2 (Text-Fig. 2) may be seen just below letter D, which represents an area where the bulldozer was not used.

Fig. 127. View of the Smoky Tower locality from above after bulldozing. Letters A, B, E, and F correspond to the positions marked by the same letters in Figs. 1 and 126 and Text-Fig. 6. The area enclosed by the letters represents the area in which sediments were removed down to the volcanic tuff layer, which is visible as the white areas to the right of letter B.


126
127

To summarize the results of this distributional study, it may be seen that the only genus found uniformly in the whole study area was *Glyptostrobus*. All other genera were restricted to specific areas. It should be noted here (see Text-Fig. 6) that there are only a limited number of angiosperm leaf remains shown on the map. Most angiosperms discussed in the systematics chapter were not collected *in situ*. In the initial exposure of the locality by the oil company and government road builders much material was pushed to either side of the hill and at the base of it. Obviously no conclusions in terms of lateral distribution can be made from this material, but nevertheless it did yield many fine specimens for taxonomic consideration.

While the unique lateral distribution shown by the fossils in the tuff horizon is easily described, its interpretation is an entirely different matter. As mentioned earlier in relation to the arrangement and disposition of *Equisetum* remains within the horizon, it is possible to speculate a relatively rapid rate of sedimentation for this horizon. Accepting this speculation, it would follow that the time and area of deposition of the plant remains found within the layer might also be more limited than usual. As MacGinite (1969) stated, it is possible for various stream-side plants to have their remains carried several miles by water without appreciably harming them. This being the case, it would be expected that either a random mixture might occur, or that a definite sorting and grading of

various genera would be accomplished by the water prior to final deposition. Experiments carried out by the author in a closed system holding approximately 200 gallons and having a controllable water source showed that twigs and branches from *Metasequoia*, *Glyptostrobus*, *Sciadopitys*, *Thuja*, and *Ginkgo*, when placed in the system and subjected to various rates of water flow, settled randomly and not in isolated areas. When various angiosperm remains were added to this mixture and also tested separately, it was found that they usually settled selectively, which may have been due to either the greater surface area or the greater mass.

Results of this experiment seem to indicate several possible interpretations of the unique lateral distribution of leaf remains in the tuff horizon. The first hypothesis is that the specimens of the various genera were not deposited by a single moving body of water, and that the general depositional basin was not subject to appreciable water currents. Both conditions hypothesized are based on the experimental evidence that agitation of a body of water containing vegetative plant remains tended to mix them thoroughly.

Excluding this possibility for the deposition encountered, the most likely remaining hypothesis in the opinion of the author is that the depositional area was relatively small and that the water was quiet. *Glyptostrobus* quite possibly was prevalent around this quiet body (this is not inconsistent with the environment in which the

extant *Glyptostrobus* is found) as is indicated by its frequency and uniform distribution in the beds. Other genera found in the beds may possibly have grown very near the area of deposition, and thus the pockets of their remains could actually represent the former position of individual plants or populations of plants. The leaves and twigs could have fallen directly from the parental source and settled almost immediately into the depositional basin. Some, however, may have been carried short distances by separate slow-moving water sources and settled almost immediately upon reaching the depositional basin. As Barghoorn (1951) properly pointed out, environmental interpretations based on suites of fossil plants must be made with extreme caution. Many factors available to students of extant plant distributions are unavailable to the paleobotanist, and thus conclusions at best are tentative. It is with this in mind that the preceding interpretation of the unique lateral distribution of plant remains in the tuff horizon of the Smoky Tower locality has been made.

Age of the Floras - Several methods for the determination of the age of sediments are available to a student of Tertiary paleobotany. These include direct age determination based on radiometric dating, and relative age determination based on stratigraphy, microfossils, and megafossils. An excellent opportunity for direct age determination was available at the Smoky Tower locality. The tuff horizon consists of pockets of silicified matrix

interspersed in a layer of unconsolidated bentonite. Purification of samples of bentonite (Chapter 3) yielded clean, unaltered samples of biotite and sanidine. Potassium-Argon analysis was done on two different samples of sanidine and one sample of biotite by Professor H. Badsgaard of the Department of Geology, University of Alberta. The two sanidine samples yielded dates of 62.5 and 61.8 million years, and the biotite sample yielded a date of 60.5 million. Dr. Badsgaard (personal communication) stated that based on his calculations and knowledge of the equipment used he felt that the dates were accurate within 1.5-2.0 million years. While the variations in the three samples run and the expressed margin of error make a precise date impossible to state at this time, the information does support the hypothesis that the flora in the tuff horizon is of Paleocene age.

Of the indirect methods of age determination available, the exposed section available at the locality was too limited to allow stratigraphic correlation with larger, well known formations. Those microfossils discussed in the preceding chapter which are identifiable have too great a stratigraphic range to make them useful in making a precise age determination. Their ranges, however, are not inconsistent with the Paleocene age assigned to the associated strata.

The specimens of the megaflora that could be assigned to species support, but do not conclusively determine, the age of the horizons to be Paleocene. *Metasequoia*

occidentalis, *Cercidiphyllum flexuosum*, *Ginkgo adiantoides* and *Thujopposites interruptus* all have broad stratigraphic ranges extending from the uppermost Cretaceous through the Paleogene. All, however, are dominant members of previously documented Paleocene floras (Brown, 1962; Chandrasekharam, 1972). More important, however, is the fact that none of the positively identified species at the Smoky Tower locality are included in the list of species which are the "best indices of Lancian age" (Dorf, 1942, p. 122). The one species from the Smoky Tower locality apparently restricted to the Paleocene, *Platanus raynoldsii*, is sufficiently tentative in its identification not to be useful as an indicator of a Paleocene age.

The fresh water pelecypod and gastropod fauna found in the blocky sandstone and the calcareous siltstone horizons at the Smoky Tower locality provide evidence similar to the two megafloras. All identifiable members of the fauna have been reported from the Paleocene, but most, if not all, of them have ranges extending from the Cretaceous through the Paleogene.

In a like manner, the data from the drilling log of the oil well at the locality supports but does not prove a Paleocene age for the fossil bearing strata. The over four thousand feet of sediments between the base of the Wapiti Formation shown on the drilling log and the fossiliferous strata is not an unrealistic thickness to reach into the Paleocene Paskapoo Formation. However, the lack of a

definitive higher marker horizon (such as the Kneehills Tuff) makes it impossible to prove.

The results of the various methods of age determination, when taken together, support the suggestion that the strata of the Smoky Tower locality are of Paleocene age. Acceptance of this is done with the understanding that assumptions and qualifications stated by various workers (Dorf, 1942; MacGinite, 1969) regarding age correlations based on fossil plant remains are valid, and conclusions drawn from such correlations in this thesis are done with this in mind.

Ecological Interpretations - As was eloquently stated by Barghoorn (1951), extreme caution must be exercised in drawing ecological inferences from fossil plant assemblages. This is particularly true in the case of floras such as the Smoky Tower floras, where a relatively small number of positively identifiable species are at hand. All ecological interpretations or correlations made between fossil assemblages and present day ones are made with the assumption in mind that organisms and communities of organisms interacted with the environments of the past in the same way as they do today.

Looking first at the flora contained in the tuff horizon, it can be seen that the modern counterparts of the genera represented there; *Sciadopitys*, *Metasequoia*, *Glyptostrobus*, *Ginkgo*, *Cercidiphyllum*, and *Zelkova*, are presently restricted to eastern Asia and Japan. Certain species of

the present day counterparts of the other genera represented in the tuff horizon; *Thuja*, *Platanus*, and *Equisetum*, are also found in the same geographic area, but are not necessarily restricted to it. Chu and Cooper (1950) reported on the native habitat of *Metasequoia* and stated that *Cercidiphyllum* was found growing in association with it. In Japan *Cercidiphyllum* is found growing in habitats adjacent to those supporting *Sciadopitys*. While some authorities question whether *Ginkgo* actually exists in a native state anymore (Dallimore and Jackson, 1966), the environment in which it is cultivated in China is certainly comparable to the native home of *Metasequoia*.

As is the case for *Ginkgo*, it is thought that only cultivated stands of *Glyptostrobus* now exist. These stands are found in wet, swampy areas, at low elevations in southern China (Brown, 1936), and it may be speculated that, in light of this, and also considering the morphological similarity to *Taxodium disticum* (e.g. production of pneumatophores), the natural habitat of *Glyptostrobus* was likely to be similar to the cultivated one. It should be noted, however, that some species of *Taxodium* (also capable of pneumatophore production) are found at higher elevations and in slightly drier regimes. Thus, inferences on the native habitat of *Glyptostrobus*, particularly in the past, must be left open to some question.

If the assumption that the plants represented by the fossils in the tuff horizon grew under similar conditions to

those of the extant species is accepted, then it may be suggested that the locality had a warm temperate climate with high summer rainfall and generally frostless winters similar to the climate of the Shu-hsa valley in China, the present home of the only native stands of *Metasequoia*. Coupling this hypothesis with the hypothesized depositional environment discussed earlier in the chapter, it is possible to construct a model for the Smoky Tower locality at the time of the tuff deposition.

The central area of deposition was probably a swampy, low-lying area with *Glyptostrobus* being the dominant arborescent species. This idea is supported by the general distribution of glyptostroboid remains throughout the lateral extent of the horizon. This small swampy area was probably surrounded by a higher, better drained area which was populated by *Thujopposites*, *Metasequoia*, *Sciadopitophyllum*, *Ginkgo* and the other associated genera. It is also possible that these other genera grew on small isolated hills within the swampy area. If the body of water was quiet as has been hypothesized, it is quite possible that transport of the remains of the upland genera was accomplished either by the deciduous twigs and leaves falling directly into the depositional basin or by their being carried by run-off following precipitation and settling almost immediately. The coal seams directly above and below the tuff horizon add credence to this hypothesized swamp environment at the time of ash deposition. Above the upper coal

seam (coal #2, Text-Fig. 2) the presence of a medium grained sandstone fining into a shale or siltstone indicates a possibly deeper and less stagnant depositional environment. This is also supported by the fresh water pelecypod and gastropod fauna which begins in the sandstone and continues upward through the siltstone. The upper portion of this siltstone contains the siltstone flora (Text-Fig. 2). This consists of a heterogenous mixture of woody angiosperm leaf remains (many fragmentary) and herbaceous aquatic remains, which would tend to suggest the possibility that the depositional environment may possibly have included deeper and certainly less-stagnant water, and that the plant remains may have been transported by a more rapidly moving water from a more distant source. The lack of coniferous remains in the siltstone flora may be taken as indicating either a major climatic change that was unfavorable to their growth in the area, or else as an indication that the areas environmentally suitable to them were no longer near enough to the basin of deposition so that their remains could be incorporated in the sediments.

Comparison with Other Major Floras - While most of the genera making up the two floras of the Smoky Tower locality are documented from other Paleocene floras, the particular make-up and proportions of them appear to be unique. Geographically and possibly geologically the most comparable flora is the Genesee flora, found roughly 250 miles south and east of the Smoky Tower locality (Chandrasekharam, 1972).

If the two floras of the Smoky Tower locality are treated as one, then the Genesee and Smoky Tower localities are highly similar. They have in common; *Metasequoia*, *Cercidiphyllum*, *Platanus*, *Glyptostrobus*, and *Azolla*. The *Metasequoia-Cercidiphyllum* combinations found at both localities and also found in modern-day central China indicate a somewhat similar environmental situation. It is interesting to note, however, that in addition to the differing proportions of the two genera at the two sites, the *Metasequoia* remains are also quite dissimilar. As pointed out in the systematic section, the differences are not deemed great enough for separation at the specific level. The relatively large quantity of drip-tips on *Cercidiphyllum* leaves at the Genesee locality, as opposed to their absence at the Smoky Tower locality, may indicate a greater degree of precipitation at the former site.

Brown (1962) gives an extensive account of the uppermost Cretaceous and Paleocene strata in various parts of North America as well as in other areas. In that paper (pp 38-39) Brown listed the various genera of plants studied by him, and the localities at which they occur. Examination of this list shows that localities from the Fort Union Formation of North and South Dakota and Montana, taken collectively compare favorably with the Smoky Tower locality strata. While the Fort Union localities, collectively, show more diversity, the major genera (excepting *Sciadopitophyllum*) represented at the Smoky Tower locality, are all found within

it. These genera include *Metasequoia*, *Glyptostrobus*, *Ginkgo*, *Cercidiphyllum*, *Thujopposites* (*Thuja*), and *Platanus*. A similar, favorable comparison may be made with the Wyoming and Colorado outcrops of the Ferris Formation, which apparently includes the Tertiary-Cretaceous boundary, evidenced by dinosaur remains and Lancian (upper Cretaceous) equivalent plant fossils found in the lower portions of the Formation (Dorf, 1942) and mammalian and typically Tertiary plant remains found in higher portions of the Formation (Brown, 1962). Further comparisons with other localities and formations listed by Brown as Paleocene show lesser degrees of positive correlation, but some correlation appears to exist in most instances. From these observations it may be concluded that the floras of the Smoky Tower locality represent a suite of Paleocene plant remains, comparing favorably with other major Paleocene floras, yet unique in both the lateral distribution of its components in the tuff bed, and in the particular combinations and proportions of genera exhibited in the two horizons. Radiometric data, though somewhat limited at present, supports a Paleocene age for the Smoky Tower floras.

Summary

Following is a list of the major points discussed in the thesis:

1. Contained within the strata of the Smoky Tower locality are two distinct megafloras, a fresh water molluscan

fauna, and at least one distinct microflora, making it possible to study the locality from a number of approaches. One of the megafloras, the tuff flora, is situated in silicified pockets of a layer of unconsolidated bentonite, making K-Ar dating for the stratum possible.

2. *Equisetum* remains from both megafloras, identified as *E. arcticum* Heer, are present in the form of both underground and aerial remains. The presence of preserved nodal and internodal cross sections in both horizons, and the presence of possible reproductive structures in the siltstone horizon represent new information about the species. The orientation of the rhizomatous portions of the *Equisetum* at various angles to the bedding plane suggests that the *Equisetum* most likely grew after initial deposition of sediments.
3. Abundant vegetative remains in the tuff horizon of material previously identified as *Thuja interrupta* allowed a thorough study of the taxon to be made. This study, supplemented by studies of similar remains from other localities, resulted in the creation of the new genus *Thujopposites* and the new combination *Thujopposites interruptus* which are used to name material with similar leaf size and shape to *Thuja* and similar leaf and branch arrangement (opposite) to *Libocedrus*, *Austrocedrus*, and *Calocedrus*.
4. Collections from the tuff horizon yielded material which

has been identified as the first record of attached needles of a *Sciadopitys*-like conifer in North America. The name *Sciadopitophyllum canadense* is given for the new material. A comparison of this material with other *Sciadopitys*-like fossils described in the literature, as well as a study of extant *Sciadopitys*, has led to the conclusion that this group of plants is distinct enough to be separated from the Taxodiaceae and placed in its own family, the Sciadopitaceae.

5. Numerous specimens of *Metasequoia* collected from the tuff horizon show characters intermediate to *Metasequoia cuneata* (Newberry) Chaney and *M. occidentalis* (Newberry) Chaney. A comparative study of this material, other material previously assigned to both species, and material of extant *Metasequoia* shows that all the fossil material is similar enough to be placed in one species. The diagnosis of *M. occidentalis* (Newberry) Chaney is emended to include characters displayed by the Smoky Tower material, and *M. cuneata* is placed in synonomy.

6. The most common species present in the tuff horizon is *Glyptostrobus nordenskioldii* (Heer) Brown. A study of this material, similar material from other localities, material previously identified as *G. oregonensis* Brown, and material of the extant species *G. pensilis* leads to the conclusion that the fossil material is similar enough to be placed in one species. Based on priority, this species is *G. nordenskioldii*, and *G. oregonensis* is

placed in synonomy.

7. Critical examination of Chaney's review of fossil *Sequoia*, *Metasequoia*, and *Taxodium* (1951) shows that separation of fossil material of these taxa must also take into consideration the genus *Glyptostrobus*. Chaney's "distinguishing characteristics for the fossil genera" are reexamined in light of more recent work, and revised where necessary (with emphasis on inclusion of the genus *Glyptostrobus*). The conclusion is reached that identification of fossil remains of the four genera is more complex than realized in 1951, and that a large suite of fossils showing numerous characteristics is necessary to identify fossil vegetative remains of the material. To discourage misidentification of material not displaying sufficient characteristics, the form genus, *Taxodiophyllum* is proposed for remains of a taxodiaceous nature, yet not identifiable to the generic level.
8. A study of the flora of the siltstone horizon shows an almost total lack of conifer remains and a dominance of angiosperm remains. Numerous herbaceous aquatic remains suggest a depositional environment somewhat different from the tuff horizon.
9. Brief examination of the microflora found in the coal seam between the two megaflora horizons shows a rather taxonomically limited assemblage, with most members identified as species known from Paleocene deposits.

10. Examination of the lateral distribution of the fossil genera found in the tuff horizon shows an isolation of many genera which is unique among known Tertiary localities. It is suggested that this may be due to a rapid rate of sediment deposition into a basin with a limited source of plant material. Thus the isolated areas of certain fossils may represent very limited populations of these taxa, the remains of which were deposited and incorporated into the sediments very near the site of their actual growth.
11. Potassium-Argon analyses, run on two samples of sanidine and one sample of biotite from the tuff horizon, yielded radiometric dates of 62.5, 61.8, and 60.5 million years respectively.
12. Based on comparison of the Smoky Tower floras with other fossil floras, examination of the stratigraphy of the locality, identification of the fossil fauna, and results of the K-Ar data obtained from the bentonite, it is concluded that the fossil bearing beds of the Smoky Tower locality are Paleocene in age.

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